Ecological responses of the endemic anole, *Anolis bicaorum*, to rapid habitat degradation on Utila Island, Honduras



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Abstract

The genus *Anolis* is composed of over 400 New World lizards belonging to the family Dactyloidae. The high diversity and rate of endemism in this group has attracted a foray of research, but the population status of many species remain unassessed and their ecological responses to anthropogenic changes unknown. My study set out to generate the first population estimates for *Anolis bicaorum*, a little known anole endemic to Utila Island, Honduras. The study compiled an extensive occurrence, abundance, morphological and ecological dataset from which to test various hypotheses around sexual dimorphism, and the effect of declining population density. During the course of study, my survey sites were impacted by varying degrees of disturbance, such as fire, deforestation and human traffic. I repeated the surveys to provide an updated population estimate from which to compare annual status and determine if abundance had declined in response to habitat degradation. In summary, my key results include 1) plotting the distribution and apparent habitat preferences of *A. bicaorum* using occurrence-based data, 2) demonstrating a significant trend of population decline in response to anthropogenic disturbance, and 3) identifying a significant reduction in sexual-size dimorphism in response to disturbance driven population declines. Overall my data advise that *A. bicaorum* be considered as Critically Endangered in accordance with IUCN Redlist Criteria, but continued research is needed to monitor future changes in its conservation status.

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Key Words: *Anolis*, lizard, Honduras, the Bay Islands, population decline, density, sexual dimorphism, ecology, conservation.

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Permissions and ethics: All methods used to collect data on herpetofauna were conducted with accordance with professional and ethical fieldwork standards. All procedures carried out in 2019, after I commenced my Master's degree, were approved by The University of Nottingham's School of Geography Ethics Panel and the University of Nottingham's Animal Ethics and Welfare Review Board (AWERB; approval number: NON.UK014). In both 2017 & 2019, research was performed under valid biological research permits obtained from Instituto Nacional de Conservación y Desarrollo Forestal, Áreas Protegidas y Vida Silvestre (ICF) in Tegucigalpa, Honduras. In 2017, research was performed under the research permit Resolución DE-MP-054-2017; Dictamen técnico ICF-DVS-169-2017; Dictamen técnico DAP-068-2017, obtained with the support and collaboration of Kanahau Utila Research & Conservation Facility. In accord, data collection and methods in 2019 were also performed under permission granted by ICF (Memorandum ICF-DVS-133-2019; Expediente ICF-187-19) for the present study-taking place in at the University of Nottingham (UK).

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Prelude

What is an 'Anole'?

The genus *Anolis* (anoles) is composed of over 400 New World lizards belonging to the family Dactyloidae. The genus is revered as an unparalleled example of tetrapod diversity (Kusumi et al. 2011) and is considered widely as among the most successful and charismatic lizard groups (Pianka & Vitt, 2003; Losos, 2009). The *Anolis* genus includes lizards of relatively small size that are strictly diurnal and primarily arboreal (Pough et al. 2001; Nicholson et al. 2012). Anoles are distinguished from other lizards by the combined presence of four primary characteristics: 1) a colourful extensible dewlap in males (present in every male and in most females); 2) sub-digital toe pads comprised of widened lamellae and setae (Losos, 2009); 3) a unique reproductive mode i.e. laying a single fertilised egg while simultaneously developing a second egg in the other ovary (Savage, 2002; Losos, 2009); and 4) by exhibiting a complete or near completely divided mental scale (McCranie & Kohler 2015).

Anoles are distributed widely from south eastern USA, the Bahamas, and the Greater and Lesser Antilles, to Mexico and southward through Central and South America, into Brazil, including many Caribbean & Pacific islands from 0 – 3750 masl (Losos, 2009; McCranie & Kohler, 2015). Throughout their extensive neo-tropical range, a species of anole can be found in almost every available ecological situation. Species-specific niches and habitat preferences are extremely variable (Losos, 2009). One species may favour isolated montane cloud forests, while another will be at home amid the hustle and bustle of a lowland urban city. I often refer to them as the 'dependable herp'; because whichever Neotropical habitat you search, you can usually encounter an anole.

Anoles range from strictly terrestrial species amongst the leaf-litter to adept and nimble climbers in vegetation and forest canopies (Losos, 2009). Activity, metabolic rates, movement patterns and behaviour can vary greatly between species populations (Losos, 1990; Logan et al. 2018). Dependent on their given niche, some anoles are active all day and bask in open sunlight, others alternate between sun and shade upon reaching optimum temperatures, while some are crepuscular and prefer dark shaded habitats (Savage, 2002).

Most commonly, anoles adopt grey-brown colouration (occasionally green) with cryptic camouflaged patterning suited for their habitat (McCranie & Kohler, 2015). All species have small circular pupils and are exceedingly visually orientated (Fleishman, 1992). Anoles have great visual acuity that is highly tuned to perceive both full-spectrum colour and ultraviolet light (Fleishman et al. 1993). Anoles are especially perceptive of the dewlap colouration exhibited by their own species (Fleischman et al. 2017). In addition to good eyesight, anoles also possess excellent directional hearing, and can detect low intensity sounds from 1000 – 7000Hz (Cantwell & Forrest, 2013). The combination of excellent colour vision, distance perception and directional hearing, provides anoles with the apparatus to detect and respond to potential mates, rivals and/or predators.

One of the four major defining morphological and sexually dimorphic features of an anole is its dewlap, characterised as a longitudinal flap of skin on the throat that is controlled through the extension and retraction of muscle cartilage (Font & Rome 1990). Of all the morphological variation observed in anoles, quite literally, the dewlap *displays* the most remarkable. Considering anoles cannot produce any sound and that, even if they could, they might not be heard amongst the chorus of diurnal birds and insects in a tropical forest; the anole dewlap is an innovative solution adapted for long-range visual communication and signalling (Ord, 2014). Literature has referred to dewlaps as a "classic example of a complex signalling system", and reported uses in species recognition, communication, courtship, territoriality and defence (Nicholson et al. 2007; Vanhoovdonck et al. 2009).

While dewlap colour and size are diverse on an interspecific level (Fitch & Hillis, 1984), its design also varies greatly within and among populations of the same species (Leal & Fleishman, 2002; Vanhooydonck et al. 2005). As can be seen in Figure 1, *Anolis* exhibit a diverse array of body shapes, sizes and colouration schemes. The diversity of anole dewlap colours is even greater than perceived by humans, as anoles, like birds, can see ultraviolet light (Fleishman, 1992).



Figure 1. A testament to the sheer diversity of *Anolis* present in Honduras. Photographed in order are the dewlaps of males and females of 12/40 species reported for the country; encountered in the region of Cusuco National Park - 1) *A. amplisquamosus*, 2) *A. biporcatus*, 3) *A. capito*, 4) *A. cusuco*, 5) *A. johnmeyrii*, 6) *A. lemurinus*, 7) *A. ocelloscapularis*, 8) *A. petersii*, 9) *A. rodriguezii*, 10) *A. tropidonotus*, 11) *A. uniformis*, 12) *A. unilobatus*. – Photos © Tom Brown.

Why study Anoles?

Anoles are leading examples of real-time evolution, replicated adaptive radiation, sympatric speciation and the power of natural selection on independent species convergence (Losos, 2009; Castañeda et al. 2014). Such a fascinating assortment in a tetrapod group not only stimulates general curiosity, but also begs for an investigation of the enigmatic factors shaping life itself (Losos, 2017).

Throughout their study, anoles have been subject to numerous taxonomic reviews. In the past, biologists have struggled to agree on the appropriate taxonomic family for this 'Iguanian - Anoline' lizard, moving it from Iguanidae to Polychrotidae (Frost & Etheridge, 1989) before settling on Dactyloidae (Losos, 2009; Townsend et al. 2011; Pyron et al. 2013). That said, some current authorities only recognise the latter as a sub-family (Dactyloinae) within the Iguanidae' (Poe et al. 2017; Torres-Carvajal et al. 2017). The past eight years have seen considerable debate, regarding whether *Anolis* should be split into eight genera (Nicholson et al 2021, 2014, 2018; Poe 2013). However, as *Anolis* is already monophyletic (Poe 2013), splitting the genus would not resolve paraphyly and thus the anole research community has continued to use the name *Anolis*, as has the dominant taxonomic authority for reptiles (Uetz 2019).

In the most recent count, 427 species of *Anolis* are formally recognised and listed on the Reptile Database (compiled and maintained by Uetz, 2019). An exceptionally high species richness and rate of endemism is documented in some regions; e.g. approximately 150 species have radiated across the Caribbean (Losos, 1994), and >250 neo-tropical species occur throughout Central and South America (Losos, 2017). To date, Honduras has 41 *Anolis* recorded, which totals nearly 10% of the approximately 400 + species known worldwide. Of the 41 species in Honduras, 20 (nearly 50%) are classified as endemic to the country (McCranie & Kohler, 2015; McCranie, 2018). This includes the six species occurring on the Honduran Bay Islands; of which three (*Anolis bicaorum*, *Anolis utilensis* and *Anolis roatanensis*) are endemic.

According to the Reptile Database (Uetz, 2019), Harrison (2014) determined that "the rate of new *Anolis* species described per decade had held steady at about 30 since the 1960s". However, with recent advances in biology (i.e. improved exploration and access to genetic sequencing techniques); by recalculation the rate of new species discovery has increased further still in the last 10 years.

In total, 79 new *Anolis* species were described since the year 2000, and 40 of these new descriptions were published since the study of Harrison (2014). Henceforward, the known diversity of *Anolis* continues to grow and the current discovery rates show little indication of approaching a plateau. Not only is the formal number of recognised *Anolis* species growing, but so is the wealth of *Anolis* associated literature (Figure 2). The first notable mention of anoles in the biological literature appeared as a brief comment by Darwin (1871), whereby he described the territorial interactions and combat of two rival males, when musing the development of his theory on sexual selection. Since then, these lizards have continued to grab the time and efforts of many biologists and interdisciplinary researchers, in light of their use in exploring a broad and widely applicable set of biological questions (reviewed in Losos 2009).

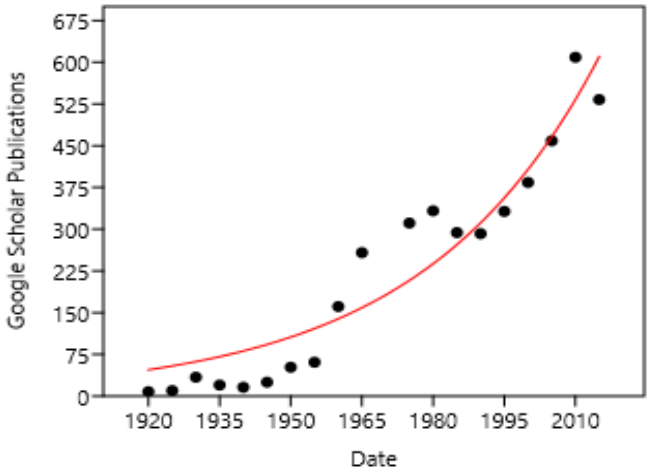


Figure 2. A graph constructed with data using the Google Scholar 'Advanced Search' feature; displaying growth in the quantity of anole related publications every 5 years from 1920-2020.

Owing to the extensive ecologically divergent nature of anoles and the high population densities that many species reach in some sites, anoles have been used as models in pioneering studies of evolutionary ecology (e.g. Roughgarden 1974; Losos 1994; D'Cruze & Stafford 2006; Singhal et al. 2007; Losos 2009). In the last century (1920-2020), Google Scholar lists over 3500 publications that contain the word Anole, *Anolis* or *Norops* in the title. Nearly 50% of these were published in the last 20 years (Figure 2), and this publication figure is by no means exhaustive. Despite the exponential increase in anole-based research, our understanding of many species remains poor and their study often 'opens a can of worms' that result in more questions and hypothesis than answers.

Ecological divergence in *Anolis*

A substantial diversity of *Anolis* species have adapted to exploit specific and narrow ecological niches; a single habitat often contains multiple sympatric species. The current consensus is that each species will only occupy a defined subset of the environment where it has adapted to be most successful (Losos, 2009). As anoles primarily occupy the same trophic level, co-existing anoles tend to partition resources and microhabitats by specialising in a specific niche (Pacala & Roughgarden, 1982).

Niche partitioning is best demonstrated throughout the islands of the West Indies (e.g. in the Greater Antilles - Losos, 2004; Pinto et al. 2008). On these islands, anole species which occupy the same niche (i.e. fulfil the same or similar ecological roles) have been placed into six "ecomorph classes" (proposed by Williams 1972, 1983; reviewed by Losos 2009). Ecomorphs are based on microhabitat preferences, morphological characteristics and behavioural traits, and are named for where in the environment you would usually encounter the anole (i.e. Trunk-Ground, Trunk, Trunk-Crown, Crown-Giant, Twig, Grass-Bush). Regardless of geographic location, species assigned to each ecomorph exhibit near identical morphological characteristics, features that are adapted to enable each anole to specialise in their specific microhabitat (e.g. long legs for running/jumping along the trunk/ground, large lamellae-full toe-pads for grip in the canopy, or short legs for agile climbing on thin branches etc.). Consequently, many species of West Indian island anoles appear and behave superficially alike, owing to the fact that similar and successful morphologies have adapted repeatedly to fill analogous unoccupied niches (Losos 2009).

Despite their close morphological resemblance however, members of the same ecomorph are not direct relatives, indicating that convergent evolution has generated the same ecomorphs multiple times (Losos, 2009; Mahler et al. 2013). Across the West Indies, anole species occurring together at each given island location, independently diverged from a single colonising ancestor, repeatedly adapting the same morphological solutions to conquer the ecological problems created by natural habitats (Losos, 2009). In essence, whereas vegetation type may vary dependent on location, often the climatic forest communities provide the same exploitable niches (ground, trunk, canopy, vegetation) which favours lizards of a specific morphology, resulting in similar and predictable evolutionary outcomes.

For that reason, Losos et al. (2003) hypothesised that anoles were persistently evolving toward the occupancy of a distinct pre-defined set of niches, and that each species allied with a specific suite of morphological and ecological characteristics that best favoured its survival in said niche.

Subsequent literature debated the expandability of the 'ecomorphs' to encompass mainland anole populations outside the islands of the West Indies (Irshick et al. 1997; Schaad & Poe 2010). However, beyond the relative simplicity of a closed stable island ecosystem, the majority of mainland neo-tropical anole species did not fit simply into a specific 'ecomorph' group (Pinto et al. 2008). Most recently, Nicholson *et al.* (2012; 2018) attempted to redefine the six 'ecomorphs' by introducing eight 'ecomodes', for which they assigned mainland populations. Despite this work being subject to some critique and resistance from the scientific community (e.g. Poe et al 2013; Nicholson et al. 2014; see McCranie & Kohler, 2015); broadly speaking, it seems that most mainland anoles generally fit one or span two of these 'ecomode' categories.

Continental habitats (as opposed to islands) provide a far greater complexity of ecological situations for anoles to access, and environmental pressures by which their adaptations are influenced (Cantero et al. 2016). These include differences in vegetation structure, population density, interspecific and intraspecific competition and predation rates (Irshick et al. 1997). Justifiably, many mainland species exhibit great variation in habitat use throughout their range, and can be constantly adapting to exploit newly available resources or in response to unpredicted change. Therefore, it may always be difficult to pigeonhole widespread species into a single 'ecomorph' or 'ecomode', as these classifications are only determined by the conditions available to each population at the given locality in its distribution.

While anoles partition their niches between species, they are also shown to partition their niches between the sexes of the same species (Butler, 2007). Biologists have had a long-running fascination with intersexual differences (Darwin 1859, 1871; Bajema 1984), with morphology being the most prominent and frequently documented sexually dimorphic difference between males and females. Sexual size dimorphism is found to exist in both the plant and animal kingdoms, where it occurs across all known taxa (reviewed by Fairbairn 1997).

Anoles are sexually different in body morphology and most prominently with regard to male-female dewlap size and colour (Butler, 2007; Vanhooydonck et al. 2009). In light of these observable differences in body size and proportion, many researchers have found evidence of sexually dimorphic behaviours, inferring that different morphologies often allude to a corresponding difference in resource use and ecology (Butler et al. 2000). Apart from intersexual differences in size, male and female anoles have been suggested to differ in a suite of characteristics; including shape (Butler and Losos 2002; Losos et al. 2003), ecology (Butler and Losos 2002), performance (Herrel et al. 1999, 2001, 2006), behaviour (e.g. escape mechanisms, Vanhooydonck et al. 2007), diet (Perry, 1996), habitat use (Irschick et al. 1997; Barquero & Arguedas 2009; Dill et al. 2013) and physiology (Orrell et al. 2004).

The existence of sexual dimorphism in the above-mentioned traits are most plausibly explained by theories first proposed by Darwin (1859, 1871) concerning sexual selection, suggesting that the adaptive pressures of different reproductive roles and the "different habits of their life" ultimately lead to intersexual resource and niche partitioning. Population density has been closely linked with sexual dimorphism and intersexual competition for resource and space (Stamps et al. 1997), suggesting that dimorphism may allow inter-sexual competition to be avoided at high population densities. This in turn, may give rise to each sex living under the influence of different environmental constraints (prey source, predators/competitors, substrate type), which can further drive the adaptation of sexually dimorphic morphology. Such theories have since been supported by various studies (Fairbairn 1997; Butler et al. 2000; Butler & Losos, 2002; Losos et al. 2003).

1: Ecological responses of *Anolis bicaorum*, to rapid habitat degradation on Utila Island, Honduras

1.1: Introduction

Islands are among the most vulnerable ecosystems on the planet, described by Cronk (1997) as a diversity and stability paradox. The geographic isolation of islands tend to generate endemic and highly specialised flora and fauna (MacArthur and Wilson, 1967), resulting in organisms that possess unusual adaptations or entirely new characteristics (Velmurgan et al. 2018). This is certainly the case for the genus *Anolis*, with most islands containing at least one, and often many more endemic species (Losos, 1994).

In the past and present day, anoles on islands have been subject to episodic and continuous forces of change. This has included natural phenomena such as extreme weather (e.g. Hurricanes - Schoener et al. 2001; 2004; Donihue et al. 2018), climate change (Leal & Gunderson, 2012; Logan et al. 2013; 2018) and volcanism (Muñoz & Hewlett, 2017), but increasingly also anthropogenic disturbance by means of urbanization, agriculture, deforestation, and socioeconomic or political actions (McCranie & Kohler, 2015). Globalisation and tourism on islands is linked not only with rising disturbance (Hall, 2010), but also the introduction of invasive species (e.g. *Anolis sagrei* – Powell et al. 2011; Tan & Lim, 2012; Helmus et al. 2014). In some localities, *A. sagrei* has been shown to impact native anoles in many ways, including by driving evolutionary change (behavioural and morphological - Kamath et al. 2013; Stuart et al. 2014), increasing direct competition for resources, and extinction rates (Brooks & Smith, 2001; Kraus, 2015).

Land-use change and invasive species are among the primary threats to biodiversity and ecosystem services worldwide (Chornesky & Randal, 2003; Turner et al. 2007; Pimm et al. 2014). However, because island ecosystems are naturally isolated, topographically restricted and usually possess a high floral and/or faunal endemicity with limited gene flow, the impacts associated with habitat degradation and invasive species on islands are disproportionately stronger and more persistent than when they occur in continental biomes (Tershy et al. 2015; Spatz et al. 2017). Understanding the evolutionary consequences of such anthropogenic change on wildlife is a newly emerging topic in biology (Smith & Bernatchez, 2008). Most studies concerning human-driven environmental impacts are motivated in part by the need to assess the conservation status of one or more species, and their response to ongoing change.

Simply put, conservation aims to prevent species and ecosystem loss (Soulé, 1985) while still managing human uses of environmental resources (Kareiva & Marvier, 2012); however, in practice those concepts prove to be a complex issue (Newbold et al. 2016). While highly sensitive species may go extinct in response to the slight habitat alterations (Case et al. 1992), those with broader environmental tolerances may persist and adjust to the changes (Cronk, 1997; Marnocha et al. 2011; Winchell et al. 2018). In order to successfully mitigate threats associated with anthropogenic change, a complete understanding of ecological mechanics, as well as the long-term interactions between native species and their environments is required.

Historic descriptions, or the first datasets for any ecosystem or species, can provide valuable information on ecological systems prior to anthropogenic change. However, such datasets are rare and efforts to determine the ongoing or future impacts of environmental change on species' are often hampered by a lack of baseline ecological and species population data. This same disadvantage limits the study of evolution, adaptation and extinction, whereby, without data on an organism's original form and ecology (Turvey et al. 2015), it is difficult to determine ecological and evolutionary responses to natural or anthropogenic pressures (e.g. intraspecific morphological or behavioural change). Missing information spans all manner of species-specific life history traits, from general ecology, distribution, abundance, behaviour and morphological data; so, the value of documenting in-situ field observations should never be underestimated. It is widely accepted that to comprehend the true magnitude of anthropogenic impact and inform appropriate conservation management, an extensive knowledge regarding the natural history of the target species and its location is first required (Collen et al. 2011).

The target subject of my research is *Anolis bicaorum*, a little studied anole endemic to Utila Island, located off the Caribbean coast of Honduras. Utila hosts a number of endemic species. While little/no formal research has been carried out to assess the conservation status of Utila's biodiversity, threats to native wildlife are likely increasing as the island continues to develop a tourist-based economy. While large western portions of savanna and mangrove habitat on the island remain relatively isolated and pristine, both deforestation and development appears to be accelerating in the eastern region where most of the hardwood forest habitat is located. In addition, populations of invasive species are also beginning to establish and are likely to spread rapidly across the island (Brown & Diotallevi, 2019). While under imminent threat, the island still presents an opportunity to gather a foundation of data from which to determine, monitor and hopefully combat the real-time effects of anthropogenic disturbance on its native species.

1.2: Study Location

Honduras is a Central American country with high biological and herpetofaunal diversity (Meyer & Wilson, 1973; McCranie, 2018). Its mainland and offshore islands encompass part of the Meso-American biodiversity hotspot; a region characterized by exceptional species richness (Conservation International, 2020). The 'Honduran' Bay Islands consist of eight islands (Utila, Roatan, Guanaja, St Helena, Barbareta, Morat, and the two Hog Islands) and 53 small (mostly privately owned) cays located from 15 – 60km off the Caribbean coast of Honduras. Collectively, they form part of a Middle American mountain complex that stretches from Sierra Madre de Chiapas (Mexico) to Sierra de Omoa (northwestern Honduras), which continues as a submarine ridge across to Jamaica (Meyer 1969; Wilson & Hahn, 1973).

Utila Island is the smallest and westernmost of the three major Honduran Bay Islands (Utila, Roatan, and Guanaja), adjacent to the Cayos Cochinos archipelago. Of the three major islands, Utila is positioned closest to the mainland, located approximately 32 km NNW from the city of La Cieba in the Honduran department of Atlántida (Figure 3). The geological history of the islands has been little studied, but it is believed they were once connected with each other and the Honduran mainland during the Miocene and Pliocene era (Vinson and Brineman, 1963). Owing to geological shifts, Utila is the only island presently situated on the continental shelf (Wilson & Hahn, 1973). The total land area of Utila is c. 44km^2 and an extant volcano (Pumpkin Hill) denotes its highest elevation at 74 masl.

Utila's dominant habitats consist of a mosaic of mangrove and swamp forests, neo-tropical savannah, coastal vegetation, volcanic 'iron-rock' shore and hardwood/palm forest (Fickert & Gruninger, 2010; Fawcett et al. 2016 – Figure 4). Swamp forests and mangroves cover more than two-thirds of Utila´s surface, largely consisting of vegetation tolerant to the influence of brackish and/or salt water (Fickert & Gruninger, 2010). Unlike Roatan and Guanaja, there is no flowing freshwater (rivers and streams) on Utila, but instead the majority of rainwater is held by seasonally flooded neo-tropical savannah, isolated ponds and within underground aquafers (McBirney & Bass, 1969). Despite its small size, the majority of Utila (especially western regions) remains vastly unexplored. These areas are largely inaccessible without a boat and hiking over challenging ground, rendering it difficult to regularly visit or study those areas comprehensively at this particular time.

There is no reliable modern consensus predicted for Utila's human population, but it ranges from 5000 – 9000 local people (Davidson, 1971; Canty, 2007). The majority of the human development is concentrated on the south-eastern side of the island. Until the 18th century, the eastern portion of Utila was almost completely covered by thick hardwood forest and mangroves (Claus & Wild 2001). Yet, owing to the arrival of English colonisers, much of this primary habitat was cleared to create space for crops and cattle pastures (Evans, 1999). Today, only relics of the original old-growth hardwood forest habitats remain, and most of these are being encroached and fragmented by ongoing agriculture and urban development (Claus & Wild 2001; Currin 2002). Most of the remaining forest habitat on the island is in fact secondary growth that has since regenerated in abandoned agricultural lands. Compared to other habitats on Utila (Fickert & Gruninger 2015), hardwood forests are disproportionately at greater risk owing to their high land-use and timber-resource value; these forests grow on dry and usually elevated land which makes them more suitable for housing development and agriculture. Mangrove swamps and neo-tropical wetland habitats have a far lower land-use potential and are often less desirable for development/agriculture due to salt-water incursion (Currin, 2002).

Considering its small size, Utila boasts an impressive 44 reported species of amphibians and reptiles (five Frogs, 20 Lizards, 14 Snakes, four Turtles and one Crocodile - McCranie and Orellana 2014; Brown & Diotallevi 2019; Brown et al. 2020); in fact, the greatest herpetofauna diversity of any island in the Bay Islands and Cayos Cochinos. Of these 44-recorded species, seven species are regarded as 'endemic', and five as 'invasive' (Figure 5 & 6). Four lizards, the Utila Spiny-tailed Iguana (*Ctenosaura bakeri*), Bica Anole (*Anolis bicaorum*), Utila Anole (*Anolis utilensis*) and the Utila Least Gecko (*Sphaerodactylus poindexteri*) only occur on Utila. Two lizards, the Honduran Leaf-toed Gecko (*Phyllodactylus palmeus*) and Bay Island Least Gecko (*Sphaerodactylus rosaurae*) are endemic to Utila and other Bay Islands (McCranie, 2018). Lastly, the Dunns Least Gecko (*Sphaerodactylus dunni*) has a distribution endemic to Honduras; recently reported for Utila (Brown et al. 2020). Currently, the island's invasive herpetofauna consist of two Asiatic geckos, the Common Asian House Gecko (*Hemidactylus frenatus* – Kohler 2001; McCranie & Rovito 2011) and the newly introduced Mourning Gecko (*Lepidodactylus lugubris* - Brown & Diotallevi 2019). Furthermore, two introduced anoles are present, the Cuban brown anole (*Anolis sagrei* – McCranie et al. 2005; McCranie & Nunez 2013) and a green anole (*Anolis allisoni*) from Roatan (Martinez & Clayson 2012). Finally, one widespread invasive amphibian, the Greenhouse Frog (*Eleutherodactylus planirostris*) also occurs (McCranie & Orellana 2014).



Figure 3. A map showing the positioning of Honduras in Mesoamerica, also highlighting the study location of Utila Island (32km from the Honduran Coast)



Figure 4. Photographs depicting some of Utila's dominant habitat types. 1) Seasonally flooded neo-tropical savannah, 2) Red mangrove swamp forest, 3) Mixed Black mangrove, 4) Volcanic 'Iron rock' shoreline and coastal palms. © Tom W. Brown

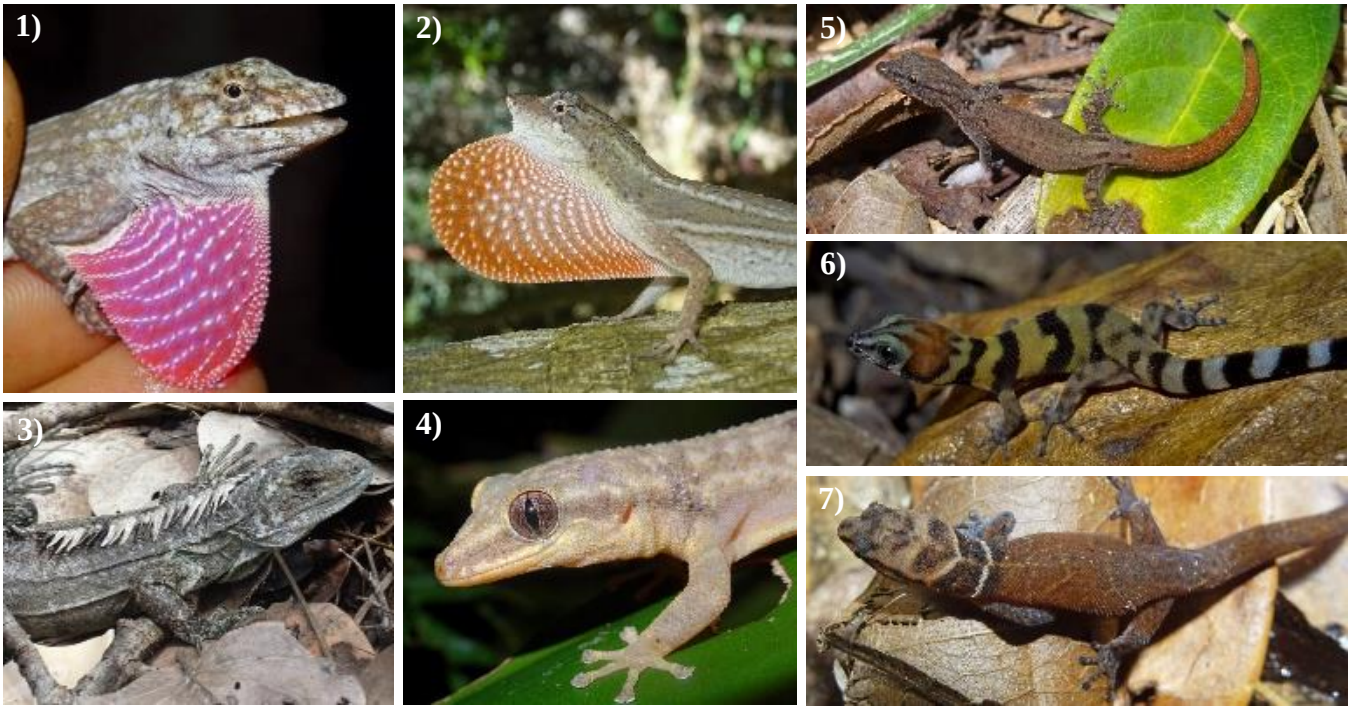


Figure 5. Photographs for the seven recorded 'endemic' reptiles on Utila Island. The species name and region they are occur as follows; **1)** the Utila Anole ***Anolis utilensis*** (Utila); **2)** the Bica Anole ***Anolis bicaorum*** (Utila); **3)** the Utila Spiny-tailed Iguana ***Ctenosaura bakeri*** (Utila); **4)** the Bay Island Leaf-toed Gecko ***Phyllodactylus palmeus*** (Utila, Roatan & Cayos Cochinos); **5)** Utila Least Gecko ***Sphaerodactylus poindexteri*** (Utila); **6)** the Bay Island Least Gecko ***Sphaerodactylus rosaurae*** (Utila, Roatan & Cayos Cochinos); and **7)** the Dunns Least Gecko ***Sphaerodactylus dunni*** (Honduras & Utila). With exception for the mangrove specialist Iguana *C. bakeri,* all other endemic species appear dependent on areas of coastal and inland tropical forest habitats. © Tom Brown

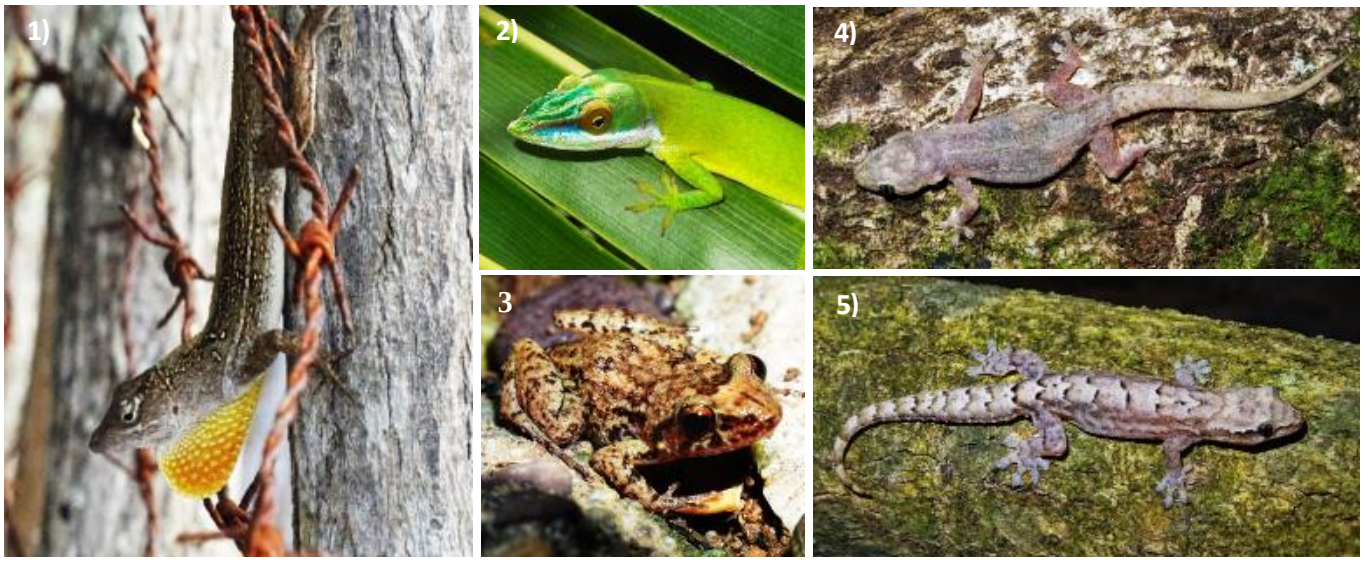


Figure 6. Photographs for the five invasive species recorded on Utila Island to date. Their species name and native region of origin as follows; **1)** the Brown Anole ***Anolis sagrei*** (Cuba & Bahamas); **2)** the Green Anole ***Anolis allisoni*** (Roatan, Honduras); **3)** the Greenhouse Frog ***Eleutherodactylus planirostris*** (Cuba, Bahamas & Grand Caymen); **4)** the Common Asian House Gecko ***Hemidactylus frenatus*** (South-east Asia); and **5)** the Mourning Gecko ***Lepidodactylus lugubris*** (Asia/Indo-Pacific). The establishment of invasive species is concentrated mostly amid the urban areas of Utila Town. The threat these invaders pose to endemic species remains undetermined, but some (e.g. *A. sagrei* & *H. frenatus*) are suggested to have induced localised population declines. © Tom Brown

1.3: Target species

Anolis bicaorum (Kohler 1996) belongs to the *Anolis lemurinus* species sub-group (McCranie & Kohler, 2015) within the *Anolis auratus* sub-clade (Nicholson et al. 2012). The closest relative of *A. bicaorum* is its sister species *Anolis roatanensis*, which is endemic to the neighbouring Bay Island of Roatan (Kohler & McCranie, 2001). Both are descendants of *A. lemurinus*, which is widespread in mainland Central America and present on Cayos Cochinos (McCranie & Kohler, 2015). Those three species form a closely related group in Honduras based on their similar external morphology (McCranie & Kohler, 2015; Figure 7).

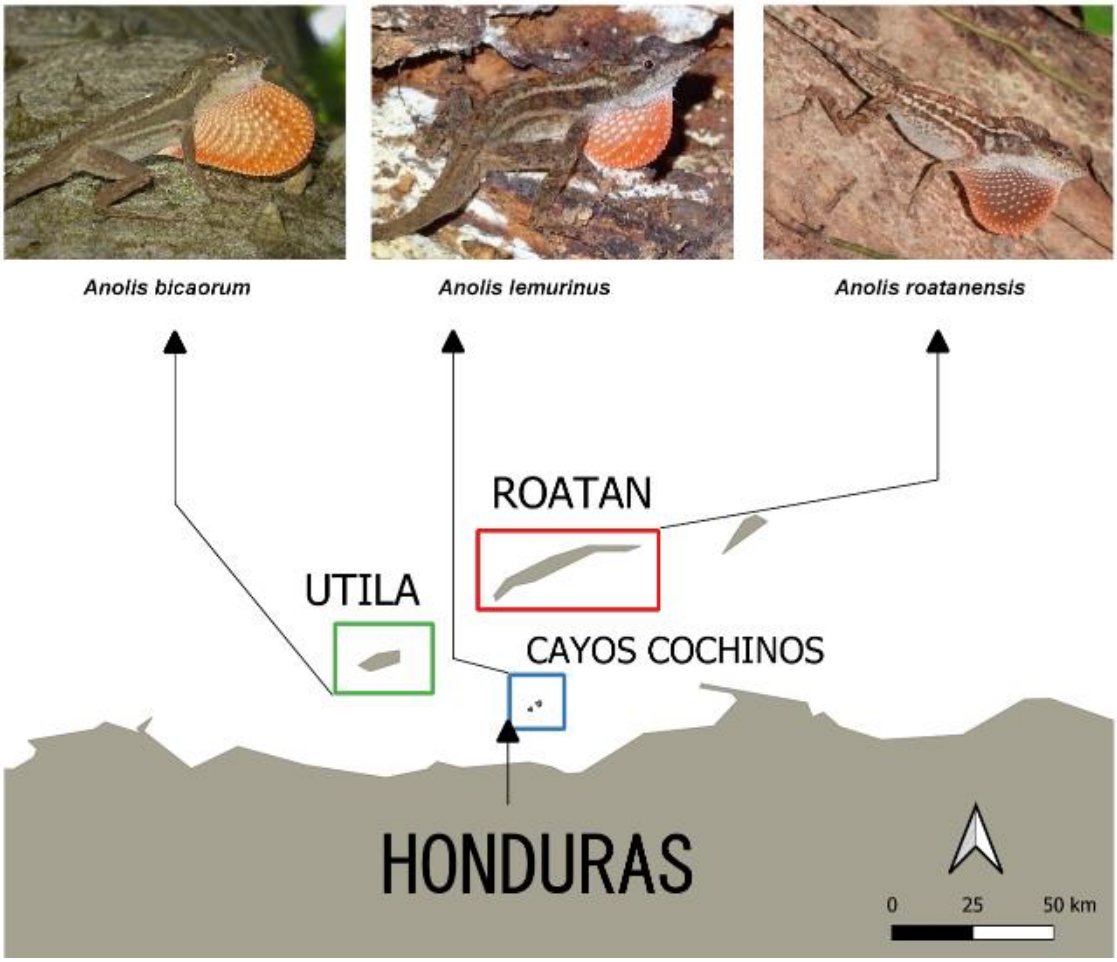


Figure 7. A map indicates the position of the Bay Islands on the Caribbean coast of Honduras with photographs that show the Honduran members of the *Anolis auratus* species sub-clade associated with each island. The widespread *A. lemurinus* occurs on Cayos Cochinos and mainland Honduras. *Anolis bicaorum* is endemic to Utila and *A. roatanensis* is endemic to Roatan. © Photos Tom W. Brown & Joel Amaya (*A. roatanensis*)

A stepping stone model of island colonisation and evolutionary radiation has been proposed for these species, with the Bay Island populations deriving from *A. lemurinus* on mainland Honduras, colonising Cayos Cochinos (*A. lemurinus*) before separate migration events introduced them to Utila and Roatan independently (Klütsch et al. 2007). The radiation of *A. lemurinus* across the Bay islands occurred within the last 10,000 years (Logan et al. 2012). In this time, genetic evidence indicates the two populations of Utila (*A. bicaorum*) and Roatan (*A. roatanensis*) have evolved in isolation to such an extent that they warrant consideration as their own distinct species (Klütsch et al. 2007). While these species appear morphologically similar (Figure 7), *A. bicaorum* and *A. roatanensis* are primarily distinguished from *A. lemurinus* by a larger dewlap that is a darker shade of red (Kohler 1996; McCranie & Kohler, 2015).

Currently, little is known about *A. bicaorum* natural history, ecology or habitat use. Likewise, literature on *A. roatanensis* is exceptionally scarce, and even detailed research into their widespread mainland relative *A. lemurinus* is surprisingly lacking. Within the available literature, most authors maintain that *A. lemurinus* are primarily found in shaded forested habitats (Kohler, 2008), however, many provide conflicting reports regarding their exact niche. Stafford & Meyer (2000) proposed that *A. lemurinus* in Belize might spend most of their time on the ground, whereas in Costa Rica, Savage (2002) stated that they rarely perch above 3m height, but Leenders (2009) maintains that *A. lemurinus* are largely canopy dwellers. With regard to the six-ecomorph classes (Williams, 1983; Losos, 2009), Nicholson et al. (2012) assigned *A. lemurinus* and its relatives to the trunk ecomode group.

In Honduras, the leading consensus is that the members of this species group are forest specialists, found perched low on trunks or active on the leaf-litter (McCranie & Kohler, 2015). The nickname 'Ghost Anoles' may also elude to the frequent ground-dwelling nature of *A. lemurinus*, because the sound of them scampering unseen across the leaf litter can resemble that of eerie footsteps in the forest. In Latin etymology, the name '*lemurinus*' literally translates as 'pertaining to the ghosts of the departed' (McCranie & Kohler, 2015). The sparse literature on *A. bicaorum* suggests that their populations on Utila are divergent in general ecology and morphology from *A. lemurinus* from the Cayos Cochinos and the mainland Honduras (Kohler 1996; McCranie et al. 2005). Logan et al. (2012) suggested that the morphological variation in those populations could be driven by differences in intrapopulation density or in predator diversity among islands.

Initial investigations by Kohler (1996) and McCranie et al. 2005) reported *A. bicaorum* as only inhabiting shaded hardwood forest environments on the eastern portion of Utila (Kohler, 1996; McCranie et al. 2005). However, I have published a number of preliminary field notes increasing knowledge of *A. bicaorum*'s natural history, including descriptions of in-situ habitat use, diet, reproduction, diurnal and nocturnal ecology (Brown et al. 2017a). These observations expanded the known distribution and elevation range for *A. bicaorum*, reporting that they also occur in fragmented patches of forest in the northern, southern and western regions of Utila (0-74 masl). In support of McCranie & Kohler (2015), I observed the seemingly densest *A. bicaorum* populations exclusively in hardwood and palm forest habitat on the eastern side.

In those dry forested regions, my observations indicated that *A. bicaorum* is sympatric and may partition its niche with its endemic congener *Anolis utilensis* (Brown et al. 2017b). Prior to that, *A. utilensis* was perhaps wrongly considered an exclusive wet mangrove habitat specialist and had only been formerly reported from 1995 – 2004 on less than 15 occasions (Gutsche et al., 2004; Hallmen et al., 2012; McCranie and Köhler, 2015). Owing to its size and relative lack of sympatric competitors (i.e. *A. utilensis* inhabits a canopy niche and *A. unilobatus* is much smaller; Brown et al. 2017ab), *A. bicaorum* is apparently active among and capable of exploiting many layers within the forest structure, from the surface of leaf litter up to 5m into the canopy.

Data deficient, preliminary observations have suggested numerous threats to *A. bicaorum*, including the destruction and fragmentation of their core forest habitat (McCranie & Kohler, 2015; Brown, 2019), as well as the newly established presence of an invasive and notoriously competitive anole, *Anolis sagrei* (McCranie & Nuñez, 2013). To my knowledge, no research has attempted to evaluate the population status of *A. bicaorum* or better understand their responses to impending threats such as land use change or invasive species. Wilson & McCranie (2004) placed *A. bicaorum* in a 'high vulnerability' category while reviewing herpetofauna in Honduras, but at that time reported that populations were stable. More recently, McCranie & Kohler (2015) observed that *A. bicaorum* appeared to be declining in altered habitat, with populations being 'seemingly down from their former exceedingly abundant category' (p 276). The apparent decline of *A. bicaorum* is unlike that observed in its close relative *A. roatanensis*, which alternatively appears to be adjusting more readily to degraded habitats on Roatan (McCranie & Kohler, 2015). Based largely on that available literature, Johnson et al. (2015) conducted a comprehensive status review of Mesoamerican herpetofauna,

which placed *A. bicaorum* in the middle portion of the highest vulnerability category, with an Environmental Vulnerability Score (EVS) of 17/21. To date the species still remains un-accessed by the IUCN Redlist. In the absence of basic ecological and population data, research has not yet addressed the capacity of *A. bicaorum* to respond to the described pressures of its changing island world.

1.4. Research Questions

My anole research on Utila was initiated with the specific focus of gathering the data needed to inform an IUCN Redlist assessment for one of the islands endemic species, *A. bicaorum* (see Brown, 2017; Appendix 2). From a species conservation standpoint, there are numerous elements of data which are essential to collect when intending to advise appropriate population management decisions. Very simply and foremost, I needed to develop a thorough understanding for the behaviour, ecology and threats to my target species, learning where it occurs, what species it interacts with and whether it specialises in a specific habitat or niche. With that knowledge, I was then able to test hypothesis concerning the relative abundance, morphology and ecological response of *A. bicaorum* populations to rapid habitat degradation.

My research started with three methodical aims and areas of investigation; 1) to opportunistically gather occurrence-based distribution data on *A. bicaorum* and its congeners to demonstrate species associations with specific habitat types and niches; 2) perform standardised capture mark-recapture surveys for *A. bicaorum* in hardwood forest habitat across multiple years to generate robust data on abundance and population density, from which to gauge trends in the conservation status of this species; and 3) collect data on the morphology of *A. bicaorum* to investigate intraspecific variation and test for density (disturbance) driven trends in sexual size dimorphism. I proceed to expand on these three objectives and the specific research questions addressed during my discussions.

As available literature indicated *A. bicaorum* occurred only in lowland moist forest habitat on the eastern side of Utila (McCranie 2015), my study first set out to confirm whether *A. bicaorum* did in fact occur in suitable forest habitat island-wide, as well as perhaps within the alternative habitat types that are available. This was important, because to gauge conservation status, my study of *A. bicaorum* density intended to calculate an extrapolated absolute abundance estimate for total population size within the area of their primary habitat on Utila.

In accordance with existing literature, I hypothesised that the distribution of *A. bicaorum* would associate with the connectivity and area of hardwood forest habitat. Because *Anolis* are ecologically diverse, I additionally hypothesised that I might detect differences in the habitat use of the five *Anolis* on Utila using the opportunistic occurrence-based data generated during my exploration. I posited the following questions, 1) Does my data support the presumption *A. bicaorum* specialise in hardwood forest habitats island-wide? ; 2) Is there an apparent difference in the habitat associations of the five *Anolis* species on Utila, or do they otherwise partition their niches within the same habitat? ; 3) Theoretically, to what extent are endemic *Anolis* currently threatened by the spread of invasive *Anolis* on Utila?

For my investigation of *A. bicaorum* population responses to habitat degradation, I used standardised survey data and various analysis to broadly investigate, 1) Does the relative abundance of *A. bicaorum* vary in different areas of hardwood forest habitat?; and 2) Is *A. bicaorum* relative abundance/density significantly changing in response to rapid habitat degradation? The latter questions are broadly imperative to determine the current conservation status of *A. bicaorum* and inform an appropriate IUCN Redlist assessment.

A final subject of major evolutionary interest is the apparent ecological and morphological divergence of *A. bicaorum* from its close relative *A. lemurinus*, especially with regard to differences in sexual size dimorphism. While some comprehensive work has been conducted on *A. lemurinus* morphology, there is currently no such data available for comparison among *A. bicaorum*. Using the morphological data I collected and available literature, I examined 1) Do *A. bicaorum* exhibit sexually dimorphic traits in morphology? ; 2) Does *A. bicaorum* follow the same evolutionary pattern of sexual dimorphism as its relative's e.g. *A. lemurinus*; 3) Does *A. bicaorum* morphology vary between different hardwood forest sites? ; 4) Is intraspecific population density a factor that drives sexual size dimorphism? ; 5) Have disturbance driven changes in density induced morphological responses in *A. bicaorum* populations?

I present comprehensive research in the following result and discussion based chapters; 2. Distribution of *A. bicaorum* and congeners on Utila; 3) Trends in *A. bicaorum* abundance and density; 4) Population Morphology, and finally 5) concluding discussion on the significance of my results with regard to the wider literature on *A. bicaorum* populations, conservation status and ecological responses to habitat degradation.

2: Distribution and habitat preference of *Anolis* on Utila

2.1: Methods and Data Collection

As part of a collaborative long-term project documenting the occurrence and distribution of herpetofauna on Utila Island with Kanahau Utila Research and Conservation Facility (KURCF), opportunistic or emergent sampling was performed in a variety of habitats to provide occurrence-based data to demonstrate the distribution and habitat preference of five *Anolis* species (*A. bicaorum, A. utilensis, A. unilobatus, A. sagrei* and *A. allisoni*).

Upon my arrival in 2016, I first set about exploring the island and learning more about its species and ecosystems. My exploratory research took place between the months of March-September annually until 2019, which involved frequently hiking (occasionally kayaking/wading) random distances through seven broadly classified regions of habitat i.e. hardwood forest, mixed swamp forest, agriculture, urban, wet mangrove, tique palm and neo-tropical savannah. I was able to perform surveys in the northern, eastern, southern and western regions of Utila, but due to the placement of the KURCF facility, my efforts were concentrated most heavily in the eastern portions of the island which were logistically and financially most accessible. The majority of my exploration started within the regions of hardwood forest habitat surrounding KURCF, before transiting through alternative habitat types during each route.

During local and remote field excursions, I recorded the ***presence*** of *Anolis* within the various habitat types on Utila. A Garmin GPS was set to 'track mode' upon leaving the KURCF, used to navigate and mark the survey route, and turned off upon return. Routes were walked at a variable pace with the general intention of encountering reptiles, and a consistent albeit sometimes subjective effort was made to detect and record *Anolis* within any habitat I passed through. Upon locating anoles, I identified the species based on its characteristics as defined by McCranie (2015), and used the Garmin GPS to record the encounter coordinates (with an accuracy of 5-10m). For each encounter, I noted the habitat type by its dominant vegetation (Fickert & Gruninger, 2015).

2.1.1: Data Analysis

Using QGIS (version 3.12.3), I produced a 2017 habitat land-cover map for Utila using seven of the nine vegetation cover metrics generated by the study of Maryon (2020); for my study, it was not pertinent to classify the area of surface water or dead mangrove (c. <3km^2) – Figure 8. Prior to generating a map, I checked the geometric validity of each multipolygon feature in the seven habitat vector layer shp. files of Maryon (2020), and amended incorrect geometries (i.e. overlapping boundaries) using advanced digitisation tools in QGIS. The area attributes of each feature comprising a habitat layer were then summed to obtain an area value for that habitats total coverage on Utila (converted to km^2). To enable measurements of overlap, the merge features tool was used to reduce the total number of attributes to a single feature.

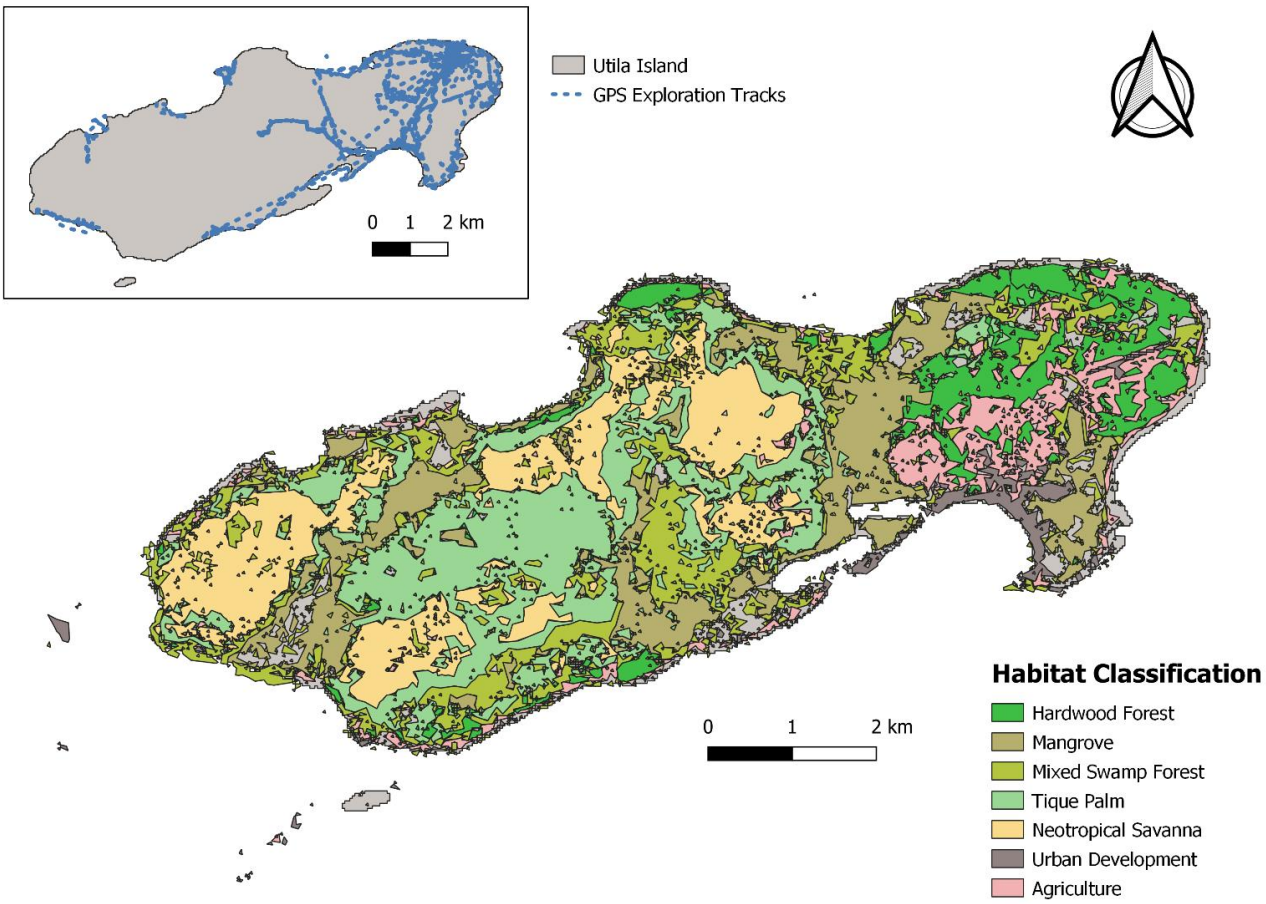


Figure 8. A 2017 habitat classification map of Utila created using the vegetation cover metrics of Maryon (2020), shows the distribution of different habitats across the island. Inset top left, a second map indicates GPS tracked survey routes across Utila from 2016-2019. This figure represents the extent of my opportunistic research within different island habitats, from which I generated occurrence-based encounter data for five species of *Anolis*.

Using Garmin Basecamp (4.7.2), I created and exported shp. files from the GPS device concerning relevant survey tracks and *Anolis* encounter points. In QGIS, I plotted the GPS survey tracks atop the land cover classification map to demonstrate where on the island my opportunistic sampling had took place in relation to the seven different habitats (Figure 8). To provide a quantitative measure of search effort within different habitats, I used the 'sum line lengths' algorithm on QGIS to measure the total length of tracked lines within, and the total quantity of them that overlapped each vegetation cover layer. This provided an output of the total distanced traversed per habitat (km), and a count of how many separate occasions I surveyed within each type. Using those values, I then computed the percentage proportion of tracked distance walked within each of the seven habitat types.

For my analysis of species distribution, the opportunistic encounter dataset containing GPS points for the five *Anolis* were plotted individually atop the habitat classification map to visualise their relative occurrence in each habitat type. To quantify the overlap between species encounters and habitat type, I used the QGIS 'count points in polygon' algorithm to determine the number of encounter points for each *Anolis* that fell within the boundaries of the seven habitat types. To account for non-uniform search effort within the seven habitat types, I calculated an unconventional measure of catch-per unit effort (CPUE), using the 'total individuals encountered/total distance walked', which resulted in amended values of 'anoles detected per tracked km' for each habitat. I visualised this data in a 100% stacked graph.

Using the counts per habitat and total encounter number (not relative to search effort), I then calculated the percentage of the total encounter points for each species within the different habitat layers. I used a paired group (UPGMA) hierarchal clustering correlation similarity index to examine relationships in the percentage proportion of species encounters relative to habitat type. Data was tested using a chi-squared test for independence (α 0.5), my null hypothesis was that the detection rate of each *Anolis* would not differ significantly between habitat types (indicating no apparent association of species with habitat).

To visualise the apparent associations in the occurrence of species with a preferred habitat type, I created a distribution map output separately for each species that included both the habitat layer containing the greatest proportion of its encounters, and the survey tracks to demonstrate a relative absence of anoles along those routes.

2.1.2: Survey Design Limitations

I intended my opportunistic methods to provide large coverage, low cost, and easily-sourced occurrence data much like that of a citizen science project, but with the added benefits of knowing where that citizen (myself) had dependably searched, and that data was reliably sourced. This was an appropriate starting point for my research given that so little information was available for island species.

Presence encounter data recorded through opportunistic means can provide useful insights into the understanding of a little-known species' ecology, as it enables large occurrence datasets across a broad spatiotemporal range to be accumulated easily and rapidly without the requirement of a strict survey design. However, as is often the case with data collected opportunistically, there are numerous predispositions to be considered that inhibit robust ecological inferences. Such datasets generally have more errors, assumptions and biases associated with them; challenges during analysis include navigating species biases, spatial biases, disproportionality in search effort and preferential recording of species, which are usually the result of unconstrained survey designs and a highly heterogeneous observation process (Altwegg & Nichols, 2019; Kelling et al. 2019; Johnson et al. 2020).

Due to the exploratory and unstructured design of my opportunistic research, I did not standardise or stratify my study of distribution by surveying routes of set lengths or by taking a reliable measurement of search effort (duration of time) spent in different habitats. The GPS was usually turned off after each survey upon returning to KURCF, which biases interpretation of tracks in assuming equal search effort was applied the entire tracked route, particularly in forest habitats close to KURCF that were repeatedly sampled. In the absence of a systematic survey design, my opportunistic results on *Anolis* distribution should be subject to close scrutiny. I proceed with several statements on the limitations of my sampling design and acknowledge implications for the interpretation and discussion of my results.

An important consideration is that my results assume that a species is absent from a tracked route, simply because I did not detect it there during rapid-sampling. While it can be relatively easy to prove the presence of a species in an area, it is nigh-impossible to say definitively that it is absent. This creates complications with interpretation, given my study did not explicitly demonstrate the absence of anoles from a surveyed route, but rather it demonstrated subjectively which habitats species' were and were '*not detected'*.

This initial problem is inextricably confounded by a second consideration; that my observation intensity was non-uniform and disproportionate between habitat types and regions (i.e. some nearby sites I visited frequently whereas other remote areas I could access only on occasion). My heterogeneous observation process did not account for numerous potentially influential variables (i.e. survey time, date, year of data collection, weather, amount of repeated tracks). These variables may have had consequences on search effort that biased the likelihood of me detecting a species within a certain habitat. Additionally, the habitat classification map were generated using satellite imagery from 2017 (Maryon 2020), and I noted substantial land cover change since then. This might apply some degree of error to the habitat associations of species distribution outputs, given they include encounter data from 2016-2019.

2.2: Results

Analysis of the GPS log specifies I traversed a total c. 412km on Utila whilst conducting exploratory research from 2016-2019; putatively equivalent to walking the perimeter (c. 54km) of the island eight times. The mean length of the 121 tracked routes stored in the GPS was c. 3.4km (SD: 11.4). The QGIS algorithm sums line length and counts the quantity of tracks which overlap a specific habitat type, providing a relative measurement of search effort (i.e. the distance walked) within each habitat. As a single track usually always overlapped with multiple habitat types and the algorithm counted tracks within each habitat separately, the total number of tracks was adjusted from 121 to 355.

My relative survey effort can be interpreted as such; I walked through hardwood forest on 96 separate occasions, during which I covered a total 244km (μ 2.5km per trip); mangrove habitats on 29 occasions covering a total 14.3km (μ 0.5km per trip); Savanna on 17 occasions covering 9.1km (μ 0.5km per trip); Tique Palm on 42 occasions covering 14.4km (μ 0.3km per trip); Swamp Forest on 77 occasions covering 54.5km (μ 0.7km per trip); Agriculture on 59 occasions covering 48.5km (μ 0.8km per trip); Urban on 35 occasions covering a total 27km (μ 0.8km per trip). Whilst surveying these routes, I recorded a total 715 encounter points for *Anolis*, c. 87% of which were *A. bicaorum*. A summary of pertinent data is shown in Table 1. Due to the absence of a strict survey design and uniform accessibility, I did not sample habitat types proportionately. There was considerable bias in the distances walked among habitat types; c. 59% of the total survey distance on Utila took place in hardwood forest habitat, the remaining effort was divided unequally between the alternative 6 habitats (Table 1; Figure 9).

Table 1. Data on the occurrence of five *Anolis* from within Utila's seven habitat types. Key in order of rows as follows: Total area (km^2) of each habitat classification on Utila; Percentage cover of each habitat type on Utila; The number of tracks within each habitat type; The tracked linear survey distance (km) within each habitat type (with a calculation of mean distance per track); Percentage ratio and proportion to which I sampled different habitats. The last five rows pertain to each *Anolis*; the total encounters and the percentage of the overall total species encounters in each habitat type.

	Utila	**Hardwood forest**	**Mangrove**	**Neotropical Savanna**	**Tique Palm**	**Swamp Forest**	**Agriculture**	**Urban**
Total Area (km^2)	41.3	3.45	6.55	7.47	9.2	7	3.1	0.98
% cover	N/A	8.4%	15.9%	18.1%	22.3%	17%	7.5%	2.4%
# of tracks	355	96	29	17	42	77	59	35
Track distance (μ per track)	411.8 (3.4)	244 (2.5)	14.3 (0.5)	9.1 (0.5)	14.4 (0.3)	54.5 (0.7)	48.5 (0.8)	27 (0.8)
Proportion of effort	100%	59%	3.5%	2.3%	3.5%	13.3%	11.8%	6.6%
Anolis bicaorum	623	451 (72.4%)	2 (0.3%)	0	11 (1.8%)	147 (23.6%)	12 (1.9%)	0
Anolis utilensis	19	15 (79%)	0	0	0	4 (21%)	0	0
Anolis unilobatus	21	10 (47%)	1 (4.8%)	0	0	3	5 (23.8%)	2 (9.6%)
Anolis sagrei	44	3 (7%)	1 (2.3%)	0	0	1 (2.3%)	4 (9%)	35 (79.5%)
Anolis allisoni	8	1 (12.5%)	0	0	0	0	2 (25%)	5 (62.5%)

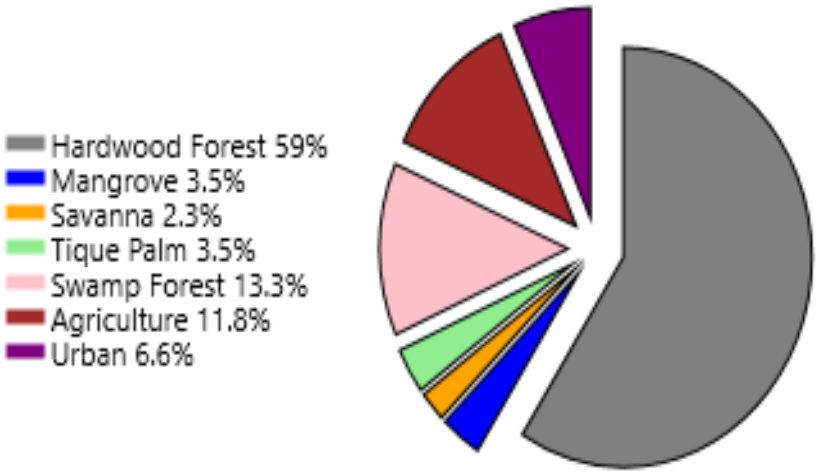


Figure 9. The percentage proportion of survey distance walked within each habitat type is used to represent relative search effort.

The percentage disproportionality of distance walked (relative search effort) per habitat type is well-visualised most simply in a pie chart (Figure 9).

To navigate the effect of disproportionately, the quantity of each *Anolis* detected was calculated relative to the total survey distance in each habitat (anoles per survey km). I considered this output to better account for encounter rate relative to search effort; but caution should still be taken when interpreting this result. The results were visualised in a 100% stacked graph to demonstrate distinctions in the habitat selection of different species (Figure 10).

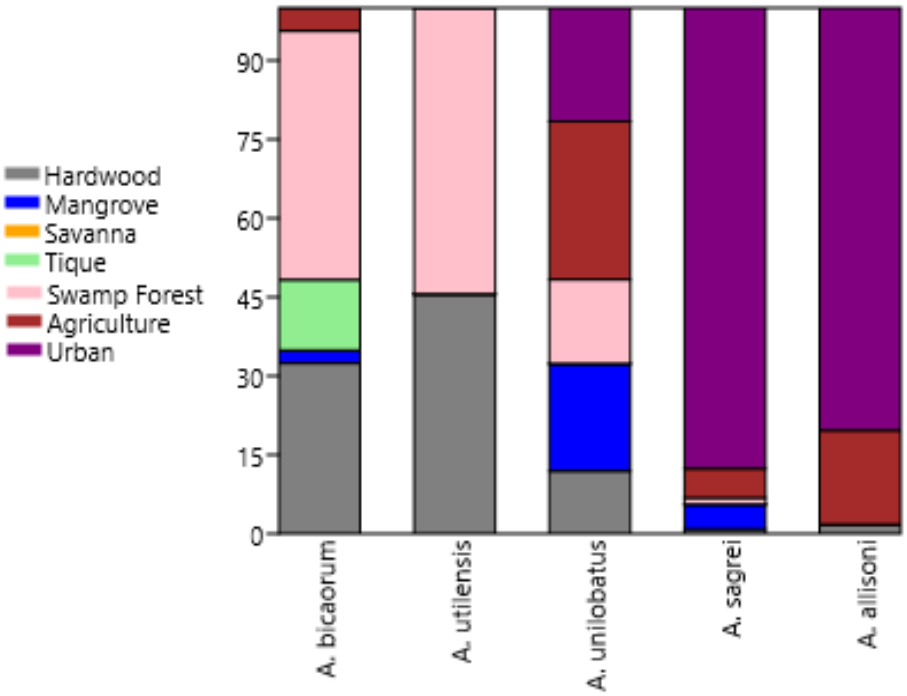


Figure 10: The percentage proportion of each species encountered relative to the total distance walked per habitat type.

To clarify relationships between species associations with specific habitat types, I used hierarchal clustering to examine correlation similarity in the percentage proportion of a species total encounters relative to each habitat type (Figure 11). This output represents the similarities between species habitat preferences, identifying species that closely associate to one another.

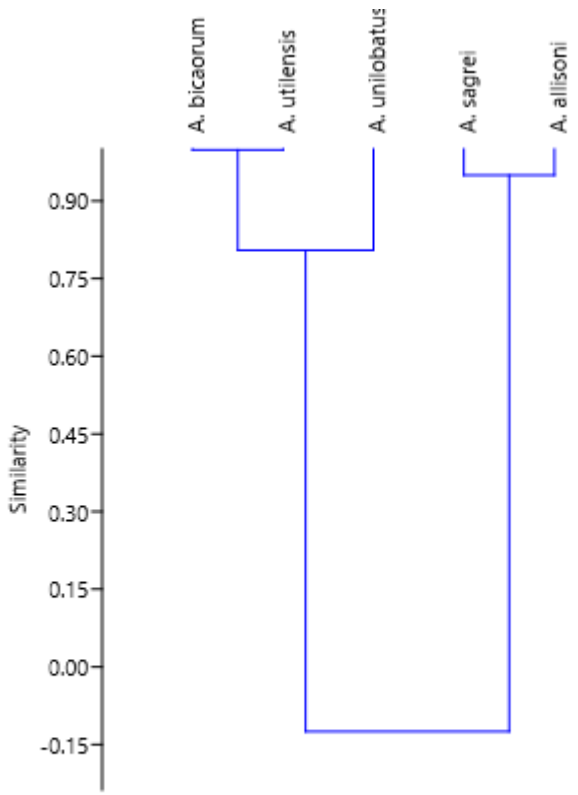
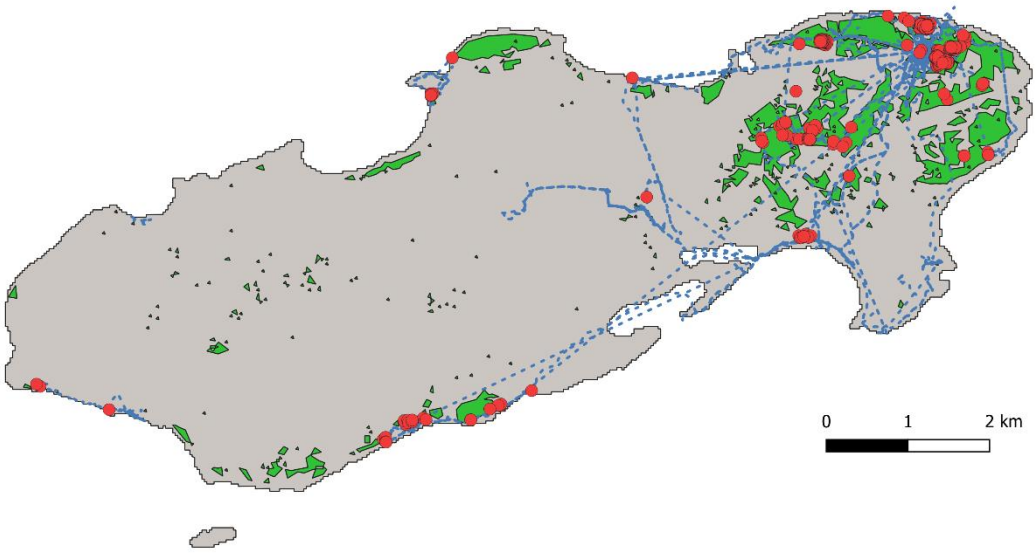


Figure 11. Dendogram generated using a paired group (UPGMA) hierarchal clustering (Correlation similarity index) on percentage proportion of species encounters relative to habitat type.

I created a series of distribution maps to visualise the known occurrence and insular range of the five *Anolis* on Utila (Figure 12 A, B, C, D, E). The GPS points of all species were plotted separately atop of the habitat layer which contained their greatest percentage of encounters (not relative to distance walked). As I did not sample the different habitat types or each region of proportionately, the extent of my opportunistic survey coverage on Utila as represented by the GPS track log (inset) and distance surveyed in each habitat (Table 1), are important components to consider alongside the following species distribution map outputs.

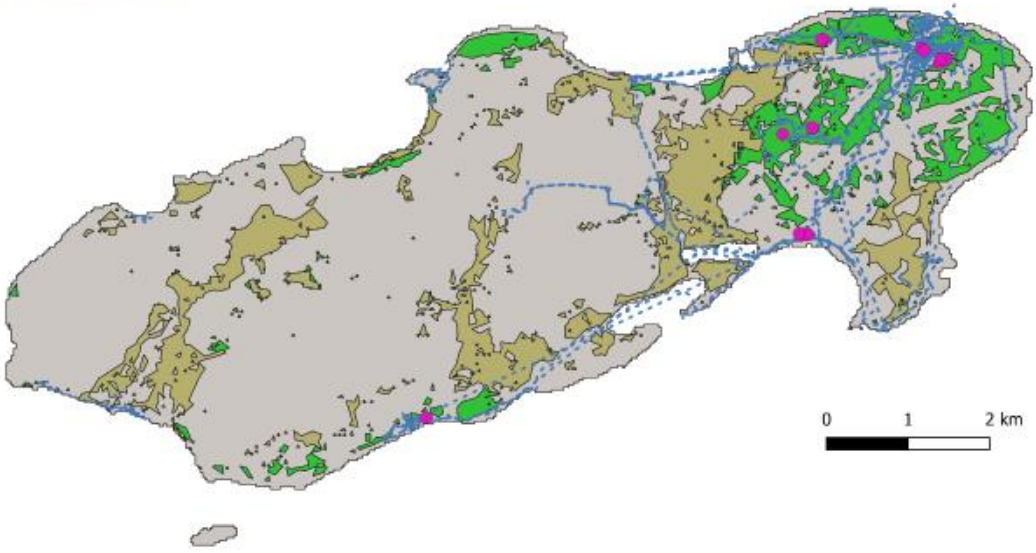
A




Anolis bicaorum
GPS Exploration Tracks
Hardwood Forest
0
1
2 km

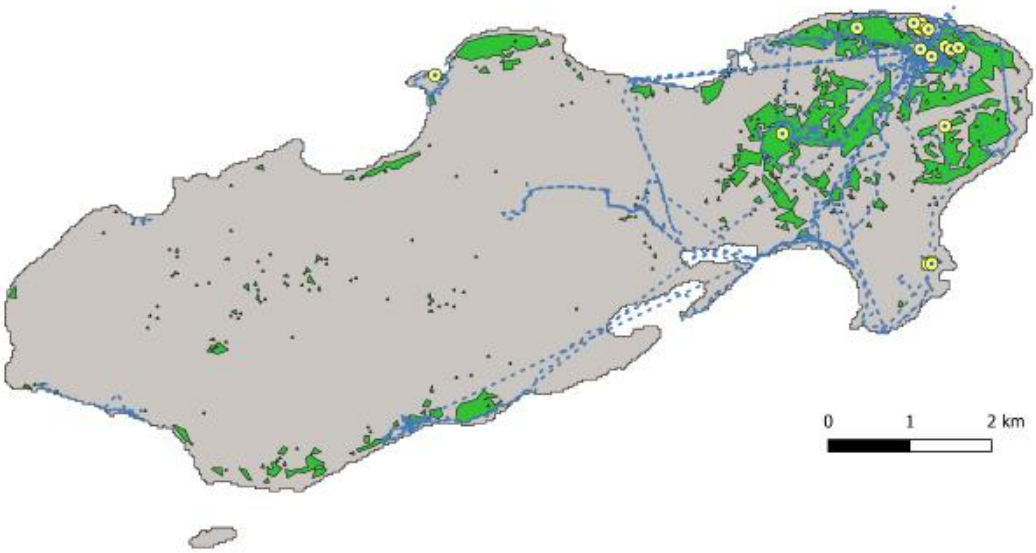
B




Anolis utilensis
GPS Exploration Tracks
Hardwood Forest
Mangrove
0
1
2 km

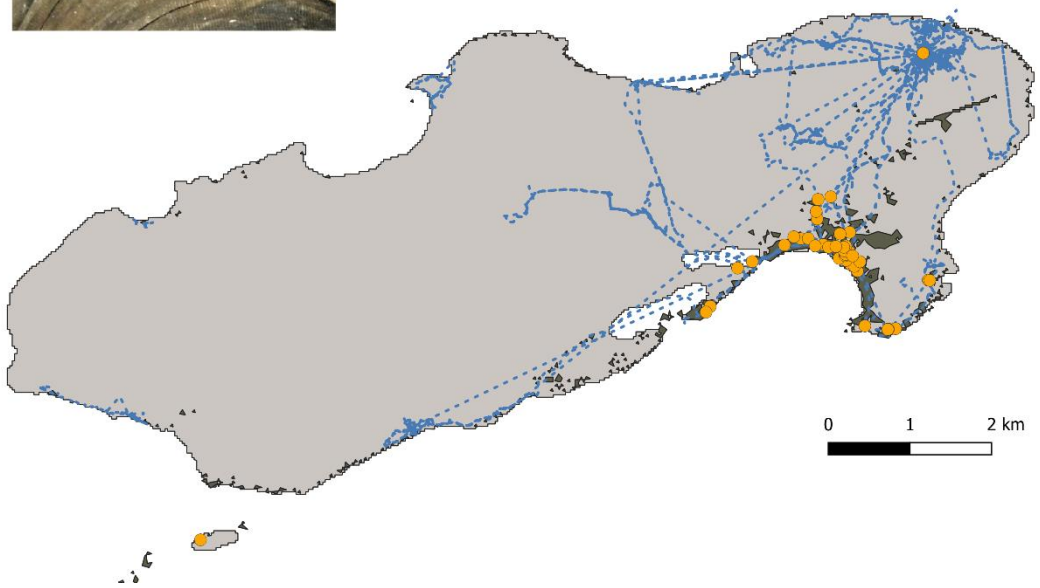
C




Anolis unilobatus
GPS Exploration Tracks
Hardwood Forest
0
1
2 km

D




Anolis sagrei
GPS Exploration Tracks
Urban Development
0
1
2 km

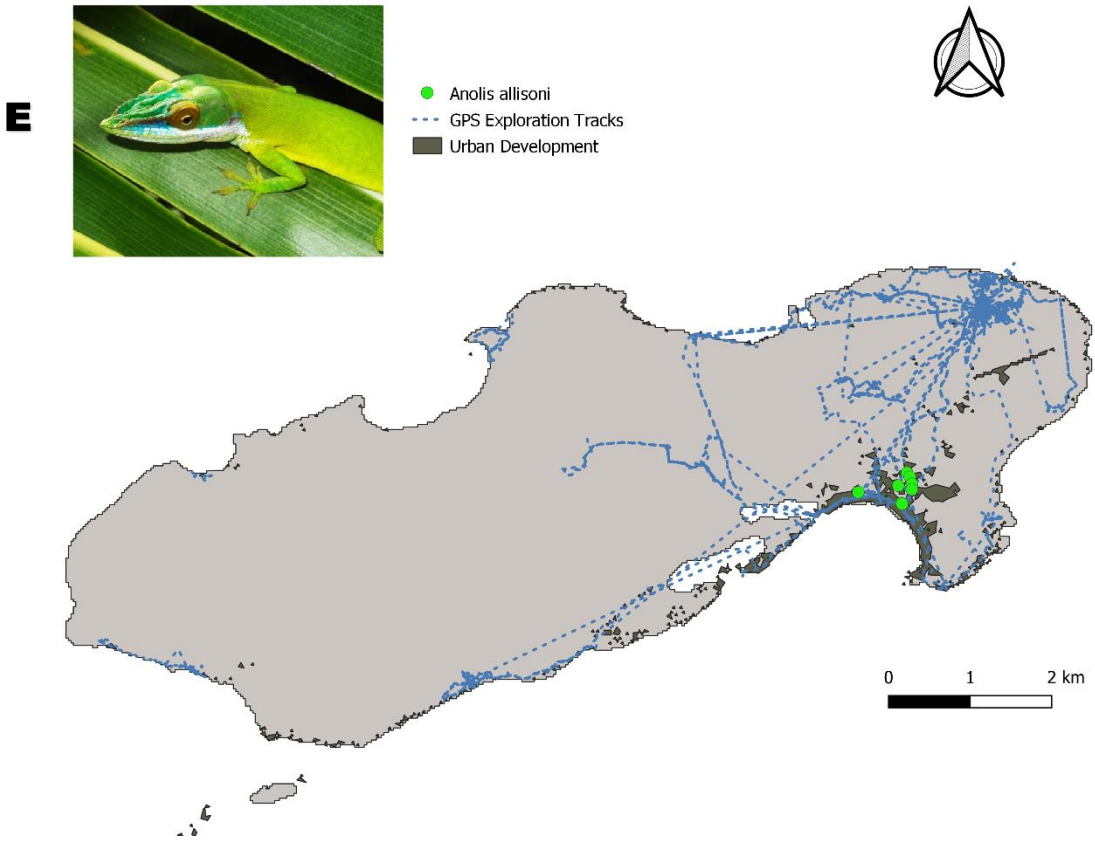


Figure 12. A series of separate distribution maps visualise the known occurrence and insular range of the five *Anolis* on Utila. GPS encounter points for endemic (**A** – *A. bicaorum*, **B** – *A. utilensis*), native (**C** – *A. unilobatus*) and invasive anoles (**D** - *A. sagrei*, **E** - *A. allisoni*) show the current known extent of their distributions on Utila and apparent habitat preference. Endemic and native species (A,B,C) tended to have wider insular distributions in natural habitats, whereas the apparent distribution of invasive species (D,E) is concentrated in the urban areas of Utila Town, presumably around their points of accidental human introduction.

2.3: Discussion

In light of many potential biases that inhibit robust ecological inferences from my occurrence dataset (see design limitations in 2.1.2), my results on species distribution warrant only an empirical discussion on the extent to which *A. bicaorum* and other species partition habitats and interact. In the absence of uniform search effort, I acknowledge that the encounter data I collected cannot be considered a strictly unbiased sample of the individuals present or absent, and hence the value and subsequent use of this data is confounded by notions of preconception.

Opportunistic methods produced species distribution outputs that are not only restricted by the limited extent of my survey coverage on Utila, but also, unintended survey biases that led to a proportionately greater focus on hardwood forest habitats (because they are predominant in the north-eastern region), and personal biases that led to a greater detection rate and preferential recording of any said species during repeat surveys in the study period (e.g. *A. bicaorum*).

In the case of Utila however, I believe my opportunistic data retains a high value because it represents the only comprehensive occurrence dataset on *Anolis* distribution to date, and it also demonstrates insular expansions in their presently reported ranges (McCranie & Kohler 2015). The presented results embody my honest personal observations of each species and thereby, based on my experiences, I believe they are indicative of species habitat preferences and their relative extent of occurrence within the confines and limitations of my study. In the following, I address my research questions (as outlined in chapter 1.4) with reference to my results concerning distribution and habitat preferences. Using my encounters so far and the wider literature, I surmise distinctions in the apparent niches of native species, and hypothetically discuss the potential future threat posed to endemic *A. bicaorum* and *A. utilensis* by the spread of invasive species i.e. *A. sagrei* and *A. allisoni*.

2.3.1: Does *A. bicaorum* specialise in hardwood forest habitats?

My raw occurrence-based data demonstrates that the distribution of *A. bicaorum* correlates largely with the 3.45km^2 of hardwood forest (Figure 12 A). However, *A. bicaorum* were also present in transitory zones of mixed swamp forest, tique palm, and very occasionally in mangrove, disturbed areas such as vegetated roadsides, fenced hedgerows and on trees that remained in agricultural land (Figure 10).

Presumably *A. bicaorum* populations on Utila remain connected, but they may be becoming increasingly fragmented by the loss of natural habitat and disturbance activities. While my observations indicate *A. bicaorum* may exhibit some tolerance and/or ability to disperse through alternative habitats, only on very few occasions did I find them far from trees, palms or a forest arrangement. As shown in Table 1, c. 96% of my encounter points for *A. bicaorum* were recorded exclusively within the islands forested habitats (the sum of both hardwood [72.4%] and swamp forest [23.6%]), reaffirming the current consensus that *A. bicaorum* exhibits dependency on closed-canopy shaded habitats (McCranie 2015; Brown et al. 2017a).

A higher proportion of my encounters relative to the distance walked apparently occurred in swamp forest habitat (Figure 10), however, I consider this result to be misleading and the result of a flaw in my survey design. The distance surveyed in hardwood forest habitat was overstated and biased by the fact I occasionally applied minimal effort to rerecord *A. bicaorum* on repeated tracks where I had previously found them in abundance; on repeat/return surveys I was more inclined to opportunistically record encounters of rarer species by GPS, for which I had fewer/no presence records in the area. Moreover, the swamp forest zones I detected most *A. bicaorum* (and *A. utilensis*) within were closely interlinked with the borders of dry hardwood forest zones, and may even be slightly misclassified by Maryon (2020). These swamp forests in the east differed greatly from those I infrequently visited in the remote western region of the island. This is an important consideration, as because the mixed swamp forest classification represents such a multifarious floral zone (including coastal white mangrove), species encounters at the locations adjacent to hardwood forest in the eastern region cannot be considered representative of species presence in swamp forest habitat island-wide.

The same can be said for those *A. bicaorum* encounters within Tique palm, which frequently interconnected with the understory of hardwood forest. However, when I searched lone outcrops of tique palm within Neotropical savanna or habitat, I never encountered anoles. As swamp forest and tique palm beyond the eastern region are surrounded largely by waterlogged savanna and mangrove (Figure 8), I advocate these ecosystems must not be considered as the preferred habitat of *A. bicaorum*. Based on my ecological observations, swamp and mangrove forests may be unfavourable because *A. bicaorum* predate arthropods that primarily dwell in the dry leaf-litter (Brown et al. 2017a, b), and savanna may act as a natural barrier preventing dispersal of *A. bicaorum* to such areas, as they reach high temperatures with very-little shade.

The seemingly deliberate occurrence of *A. bicaorum* in closed canopy hardwood/palm forest always juxtaposed its relative absence in alternative habitat types. I thereby consider *A. bicaorum* a specialist of hardwood forest habitat, given the preponderant majority of its populations were detected in this specific habitat type. McCranie & Kohler (2015) only encountered *A. bicaorum* from the eastern portion of the island in lowland moist forest formations where the majority of the hardwood forest is concentrated. Figure 12A improves on the work of Brown et al. (2017a) by providing a distribution map for *A. bicaorum* that solidifies the expansion in known range. As only 3.45km^2 of hardwood forest habitat is available on Utila, this result has potentially significant implications for the conservation status of *A.*

bicaorum as a single island endemic. Present literature and my opportunistic results infer that any meaningful conservation assessment of *A. bicaorum* should focus research efforts within hardwood forest habitat, to determine the response of populations to anthropogenic threats within the primary portion of its range.

2.3.2: Do native *Anolis* exhibit habitat preferences or otherwise partition their niches?

Besides *A. bicaorum*, another endemic (*A. utilensis*) and one well-established native anole (*A. unilobatus*) are present on Utila (Figure 13). *Anolis utilensis* was also only known from the eastern portion of Utila (McCranie & Kohler, 2015), but my most recent observations extend this range to include the southern side (Figure 12 B). No information was previously available on the island range of *A. unilobatus* given its widespread distribution in Central America, but my results affirm its occurrence in the north-eastern region of Utila (Figure 12 C).

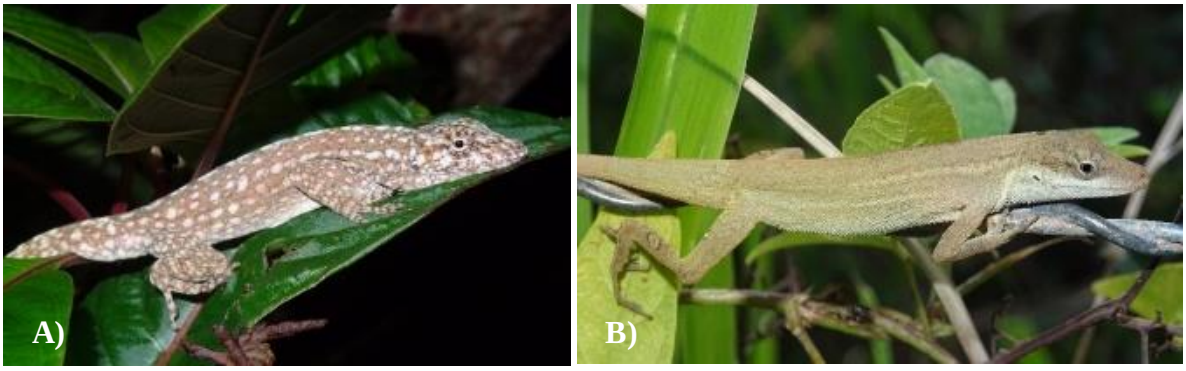


Figure 13**. (A):** Male *A. utilensis* pictured in its sleeping position on a low hanging broad-leaf. **(B):** Male *A. unilobatus* perched on barbed wire, and active diurnally among the grassy verges of agricultural land.

Much like *A. bicaorum* (Figure 12 A), I found the majority of my *A. utilensis* and *A. unilobatus* encounters interrelated mostly with hardwood forest (Figure 12 B & C), however, my observations did suggest some potential differences. In contrast to *A. bicaorum*, I only recorded 19 *A. utilensis* and 21 *A. unilobatus*. The more cryptic nature of *A. utilensis* and its tendency to use perches high in the canopy likely results in it more frequently evading my conventional visual-encounter methods, though it seems probable that this species also occurs at an overall lower density (Brown et al. 2017b). Likewise, *A. unilobatus* being the smallest and most slender of the *Anolis* on Utila, might also evade detection in the open grass-bush agricultural

habitats it seemingly prefers, however, I conceive it is surely more abundant than my results may suggest. Notably, *A. unilobatus* was only found in forests where *A. bicaorum* abundance appeared lower, perhaps indicating that *A. bicaorum* is a superior competitor when present. *Anolis utilensis* was usually present where *A. bicaorum* thrived, but did not appear to directly compete due to clearer partitioning of their forest niches. The presence of *A. unilobatus* within those forest habitats may be an indicator of canopy degradation or nearby agricultural land.

As I never observed *A. utilensis* in a forest unpopulated by *A. bicaorum*, and only rarely found either endemic species occurring sympatric with *A. unilobatus*, the distribution of *A. unilobatus* should be different from that of *A. bicaorum* or *A. utilensis* at a fine scale. The apparent distinctions in habitat selection are shown in Figure 10 that removes the disproportionate bias of search effort in hardwood forest, to better represent the preference of *A. unilobatus* for alternative generalist habitats.

Whereas both the endemic *Anolis* were located consistently within hardwood and select regions of nearby mixed swamp forest, relative to my search effort, I frequently detected *A. unilobatus* on the fringes and fence posts of agricultural, roadsides and suburban habitat consisting of grass/bush, and only occasionally deep within secondary and coastal forests (Figure 10). My observations of *A. unilobatus* suggest that it is more tolerant of open and degraded habitats, whereas *A. bicaorum* and *A. utilensis* were sympatric and specialise strictly in closed canopy forest habitat (Figure 11; Brown et al. 2017b). While these three species all utilise forest habitats to some degree, I hypothesize that there is little current competition between Utila's native anoles, as each appear to select slightly different niches. This division may reflect the ghost of competition past, whereby previous competitive interactions have shaped the habitat preferences and niche adaptations observed in these species today.

2.3.3: To what extent are endemic *Anolis* threatened by invasive congeners?

As it stands, compared to land use change, the impact of invasive *Anolis* on endemics such as *A. bicaorum* seems relatively small, and a thorough investigation of such would be premature given that the frontline populations of both species have yet to directly interact. Hypothetically, in the long-term future, invasive species could pose a considerable threat to endemic *Anolis* populations via competitive interactions, especially as urbanisation and habitat degradation

increase on Utila. Considering this risk, I use my encounters and existing literature to conjecture hypothesis concerning potential future interactions of endemic and invasive species.

Anolis sagrei Duméril & Bibron, 1837, is native to Cuba, the Bahamas, and some adjacent islands in the Caribbean (McCranie & Kohler, 2015). In the modern age, this species has greatly expanded its range and is regarded as a successful invader (Wilson and Porras, 1983; Kolbe et al., 2004; Kraus, 2009; Tan and Lim, 2012; Brown & Arrivillaga, 2017). The rapid flexibility and ability of *A. sagrei* to exploit urban environments has driven an extensive spread in its distribution, facilitated inadvertently by human movement and exportation of trade related cargos (Helmus et al. 2014). Currently the species is reported as 'alien' in more than nine countries (GISD, 2020). The occurrence and distribution of *A. sagrei* in Mexico and parts of Central America is well documented, though to date, the independent origins and relationships of *A. sagrei* throughout this range is a topic of great interest, as it is unclear whether humans introduced them (Kraus, 2009). The species has been known from the Bay Islands (Roatan) for over 60 years (Meyer, 1969; Wilson & Hahn, 1973; McCranie et al. 2005).

While it is unknown precisely when *A. sagrei* was first introduced to Utila, it has been present for at least eight years (McCranie & Kohler, 2015). As shown in Figure 12 D, currently this invader is abundant throughout the ca. 1km coastal stretch of Utila Town, and is observed to have dispersed a >1.5km radius from its presumed initial point of introduction (Utila ferry dock) via buildings, gardens, forest and mangrove habitat. So far, its spread appears mostly confined within urbanised areas, but I did detect *A. sagrei* on isolated occasions far from the region of Utila town, which may represent individuals branching out to establish at new localities via accidental human transportation; this includes one male individual from the eastern region of Pumpkin Hill, as well as populations on Pigeon Cay, a miniscule island less than 1km off the south coast of Utila only accessed by boat (Brown & Diotallevi, 2019).

The establishment and future spread of invasive *A. sagrei* populations on Utila is potentially a major concern for the endemic *A. bicaorum*. Considering that *A. sagrei* is exceptionally well adapted to urban environments and may readily exploit natural habitats too, it should be expected that this species will increase in synergism with island development; exploiting newly created disturbed environments.

The main concern is that, as primary forest habitats are further encroached upon and degraded, *A. sagrei* could eventually out-compete and displace *A. bicaorum* in its core habitat (Brown, 2018). Though I did not observe any real-time interactions between these species on Utila, across the extensive range of *A. sagrei*, numerous reports associate their spread with the decline or changing ecology of native anoles (Kamath et al. 2013; Stuart et al. 2014; Kraus, 2015). The most studied invasive populations of *A. sagrei* are those occurring in Florida, USA, which have had negative effects on the endemic green anole, *A. carolinensis*, reportedly pushing it towards extinction or higher into the canopy (Losos et al. 1993; Losos & Spiller, 1999). In the future, it seems plausible a similar competitive interaction could ensue on Utila, assuming that both *A. bicaorum* and *A. sagrei* may compete for resources within an analogous trunk-ground niche (Nicholson et al. 2012; 2018).

The most recent introduction of *A. allisoni* on Utila (Martinez & Clayson, 2012), could add further complications. My observations suggest populations of *A. allisoni* are established on buildings and trees in urban and sub-urban environments (Figure 12 E), which supports recent confirmation of their establishment provided by Brown & Diotallevi (2019). However, compared to *A. sagrei*, they appear to be much less abundant and so far relatively localised.

As *A. allisoni* occurs natively on Roatan alongside the closely related, *A. roatanensis*, it may not be a significant threat or competitor to *A. bicaorum*. However, my observations suggest *A. allisoni* could more likely infringe on the higher canopy niche of *A. utilensis*, a species which is absent from Roatan (where *A. allisoni* occupies a trunk-crown niche).

Figure 11 demonstrates a high similarity in the preferences of both invasive *Anolis* for urbanised habitats, whereas both endemic *Anolis* closely associate and exhibit preference for hardwood/swamp forests. If forest habitats become continually degraded and closer to urbanised regions, I hypothesise that the combined establishment of *A. sagrei* and *A. allisoni* may eventually affect both Utila's endemic species differently, and while I cannot confirm it using current data, it is without doubt a hot-conservation-topic for future investigation as they spread. My results present the baseline data from which to now monitor invasive *Anolis* as they encroach on natural habitats and potentially affect native species (Figure 12 D, E).

3: Trends in *A. bicaorum* Abundance and Density

3.1: Methodology

In July 2017, three sites were established that included and surrounded the north-eastern region of Pumpkin Hill (i.e. PH1, PH2, PH3), and a fourth, further afield, on-route to a location known as Ironbound (IB1) – Figure 14.

The sites were chosen following initial opportunistic surveys on the basis that 3/4 were undisturbed hardwood forest habitats; all of which were readily accessible and had observable populations of *A. bicaorum* present. Three line transects of variable set length were surveyed at each site and resampled for three consecutive days to enable a Capture Mark Recapture (CMR) and distance sampling study. While broadly classified as tropical forest, the four selected sites and transects within them are characterised by different floral compositions, understory structures and elevations. Each are representative of the slightly different hardwood forest types on Utila (i.e. coastal, broad-leaf and palm-dominated). Surveying a range of compositions within the eastern core of that remaining habitat was important as this study intended to produce representative population estimates to extrapolate across the total area of hardwood forest on Utila; identified as the primary habitat of *A. bicaorum* (Figure 12A; 2.3.1).

When my standardised study was initially planned in 2017, it was not anticipated that dramatic land-use change might occur at the four selected survey sites; the original intention was to investigate population size and morphological variance, not abundance trends. The rate of disturbance then was low, and all the sites (excluding PH3) were considered remote and wild areas of forest that seemed untouched by human activity to any great degree. However, an unforeseen pivot point occurred in early 2018 when plans to develop Pumpkin Hill road and provide better access to the region were approved and initiated. By June 2018, the once narrow forested dirt road had been developed and widened with improved access leading from Airport Road to the northern beachfront (visible by satellite – Figure 15).

Fresh access to the region of Pumpkin Hill was quickly followed by widespread clearance of forest habitat in expectation of land sale for development projects. This action indirectly affected all of my survey sites to different degrees, which enabled me to expand the scope of my study to examine changes in abundance and responses to disturbance. Descriptions of the four sites (twelve transects) in 2017 and their 2019 level of disturbance is as follows (3.1.1).

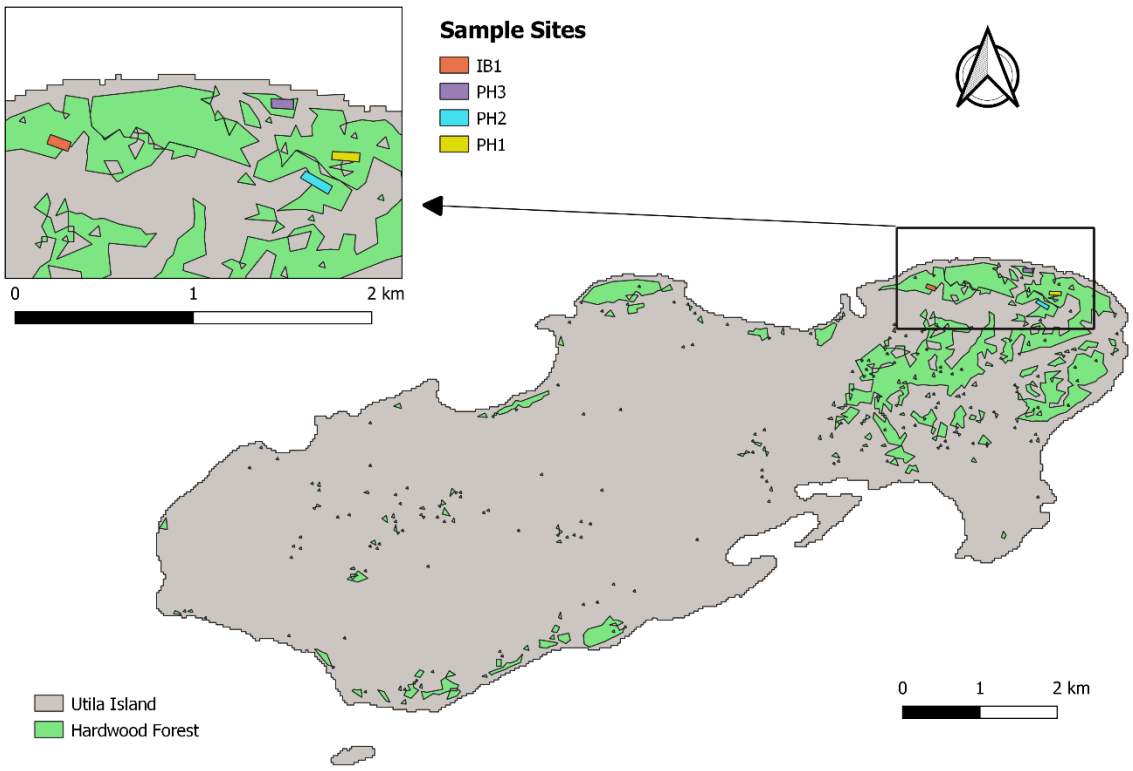


Figure 14. A map of Utila showing the location of the four selected survey sites in the north-eastern region, and the distribution of hardwood forest – a total 3.45km^2 (Maryon 2020).



Figure 15. Google Earth satellite imagery focused on the north-eastern portion of Utila, shows the locations of the four survey sites in 2017 and 2019. Close comparison of these images reveals a visibly widespread increase in disturbance since 2017, following the development of a new road to Pumpkin Hill (clearly visible in 2019 imagery).

3.1.1: Site Descriptions

Site 1 (PH1) is located at the summit of Pumpkin Hill (GPS: N16° 07.196' W86° 52.903' – Figures 16a & b), an extant volcano and the highest point on Utila at 74 masl. The habitat of the hill is Tique palm (*Acoelorrhaphe wrightii)* dominated mixed broad-leaf forest situated atop basaltic volcanic rock. PH1 Transect 1 follows a little-used forested path for 150m along the defined ridge of the hill. The vegetation along the ridge is almost entirely *A. wrightii* palms, and the terrain quickly slopes off either side. Transect 2 and 3 are located in the denser forest running parallel on the steep southward facing slope. That hillside topography made the terrain rather difficult to traverse. Iconic features of site PH1 include two mature Strangler Figs (*Ficus aurea*) grasping onto large volcanic boulders that shape the upper hillside. The leaf-litter throughout is thick with dried palm leaves and detritus, and the understory vegetation is dense and structurally complex. Mature vines run upwards from the ground to the canopies of large trees, and the smooth twisted trunks of competing *A. wrightii* palms slope at various angles reaching for sunlight. The dominance of *A. wrightii* palms at this site likely relate to its elevation, exposed windy climate and steep rocky topography, but a mixture of flowering broad-leaf trees have also taken hold and form the canopy above the sheltered slopes of the hillside. Overall, the habitat is one that appears unique in its growth and form on Utila. This remote hilltop is seemingly an important stronghold for island endemics (Brown et al., 2017ab).

In November 2018, an uncontrolled forest fire spread rapidly from agricultural lands at the base of Pumpkin Hill upwards towards the summit. The fire rapidly consumed the majority (>75%) of leaf litter across site PH1, and caused substantial heat damage to understory vegetation, palms and larger trees on transects 3 and 2. On those transects, the fire cleared the understory and created large canopy openings in some areas, reaching such intensity that it may have killed much of the biodiversity present (Figure 17 – inset bottom left). At this site, the fire may have had direct effects on anole abundance by mortality, and indirectly by reducing understory vegetation and prey availability in the leaf-litter. In addition to that, Pumpkin Hill has been subject to an increase in human traffic, largely owing to its elevation affording it unparalleled views of the entire island. Since the presence of the new road to the region in 2018, an influx of locals and tourists have started to explore and visit the hill. While most people simply pass through on foot without intention of causing prolonged disturbance, this unregulated increase in human traffic may still contribute to habitat degradation.

Site 2 (PH2) was located opposite from the base of Pumpkin Hill (33-46 masl), within mixed composition broad-leaf forest (GPS: N16° 07.121' W86° 53.000'), consisting largely of spikey yellow-trunked trees 'Prickly-yala' (*Zanthoxylum sp*), Gumbolimbo trees (*Bursera simaruba*), mature palms including *A. wrightii*, and other native fruiting trees (e.g. Yellow-Hog plum *Spondias mombin*). The habitat most closely resembles that of transect 2 and 3 PH1, but differs in that its terrain is flat on a gentle gradient and characterised by its frequent low rocky outcrops protruding from the leaf-litter (Figure 16c). The forest interior and understory is compact with the leaves of large palms and broad-leaf saplings. Both light levels and temperature within the forest interior was reduced by vegetation density. Mature vines hung down from the largest trees and a thick coat of leaf-litter carpets the ground and rocky outcrops.

In September 2018, large scale deforestation (tree-felling) and understory clearance first began at site PH2, whereby the dense palm dominated understory, mature vines and saplings were entirely chopped back and burnt systematically in piles (slash and burn). Over 30 large trees were felled throughout the site, but disturbance was concentrated to create an open clearing in the plots centre. Here, volcanic rocks were levelled to provide access and the land burnt clear to prepare it for development (Figure 17). As of 2019, this forest habitat bore little resemblance to its former quality (Figure 18). Partial regrowth of some palms had occurred, but rapid growth of pioneer plants (indicators of disturbance) had taken over the open deforested areas.

Site 3 (PH3) was located <100m from Pumpkin Hill beachfront (4-6 masl) parallel to the northern coastline (GPS: N16° 07.351' W86° 53.091'). The site encompasses transitioning coastal forest, composed mostly of tropical almond trees (*Terminalia catappa*), but dotted with rogue trumpet trees (*Cecropia peltata*), coconut (*Cocos nucifera L.)* and tique palms (*A. wrightii*). The site is bisected by a road leading to the beachfront, and was considered semi-disturbed at the time of selection in 2017. Present at the centre of the site besides the road, Transect 2 includes a derelict 4x2m concrete shed, a breezeblock wall, and a 15x15m plot of land cultivating plantains. The surrounding habitat is characterised by the evenly spaced trunks and windswept canopy of *T. catappa*, open understory scattered with small saplings and a bulky almond based leaf-litter coating porous volcanic outcrops (Figure 16d). On Transect 3, flowering Beach Spider Lily (*Hymenocallis littoralis*) and Pink Morning Glory (*Ipomoea* sp.) carpets the region before transitioning into a white sandy beachfront that is classically framed by coconut trees. Transect 1 was furthest inland and had the densest understory, composed of

T. catappa and *C. peltata* saplings, tique palms and large fallen branches. Despite the canopy above, leaf-litter was sparsely distributed throughout the site and bare soil was rife with rabbit sized holes belonging to the Blue Land Crab (*Cardisoma guanhumi*). The lack of understory vegetation across the majority of the site is presumably due to long-term land management by the owners of nearby houses.

In August 2018, the widening of the existing road to Pumpkin Hill beach impacted site PH3 through the felling of <10 roadside trees in its construction, and since through increased human road traffic and additional nearby coastal housing development. In both 2017 and 2019, I still consider the site a semi-disturbed coastal forest, of better or similar quality to that along much of Utila's occupied coastline.

Site 4 (IB1) was located the furthest from Pumpkin Hill (ca. 1.5 km linear distance), within a mixed broad-leaf forest site on route to a swampy mangrove locality known as Ironbound (GPS: N16° 07.236' W86° 53.768'). Ironbound is a lowland coastal region (12-22 masl) composed by a mosaic of habitats including mangrove, savannah, swamp and forest, largely carpeted by jagged 'iron-like' volcanic rock (for which it owes its name). This perilous rocky substrate was dominant underfoot at IB1, and porous cavities congregated pockets of leaf-litter in large volcanic blowholes. The area of forest was composed of Gumbolimbo (*B. simaruba*) and another unidentified broad-leaf tree (*Ficus* sp.), but present also were Coconut palms, native flowering shrubs, *A. wrightii* palms and numerous fruiting trees including Avocado, Grapefruit and Nancy Berry. Transect 1 was adjoined to a small trail that led through the forest, and in its centre passed down through a marshy basin thick with swamp vegetation growing in the mud. Transects 2 and 3 crossed the forested volcanic plains where trees and *A. wrightii* palms grew opportunistically wherever they could whittle space in the rock (Figure 16e).

In May 2019, local farmers cleared the entirety of understory vegetation and >30 understory palms, to provide better access for herding cattle and in preparation for expanding agricultural lands. This action completely removed the understory structure of the forest, leaving the forest looking bare, and visibly less dense. Other actions included the clearance and burning of swamp plants in the marshy basin on transect 1. Notably however, no fires were set within the denser forest and the majority of mature trees were left untouched.



Figure 16a. A photograph of Pumpkin Hill, an extant volcano and the highest elevation on Utila at 74 masl. This palm dominated broad-leaf forest is an essential habitat for biodiversity.



Figure 16b. An image taken at site PH1 Transect 1 in August 2019; depicting the characteristic smooth slant trunks of mature Tique Palm and the dense sapling dominated understory.



Figure 16c. An image taken at site PH2 Transect 3 in August 2017; a dense mixture of broad-leaf trees and palms provide a cool dark microclimate.



Figure 16d. An image taken at site PH3 Transect 2 in August 2019. A semi-managed coastal forest with a near monoculture of windswept Tropical-Almond trees and bright open understory.



Figure 16e. An image taken at site IB1 Transect 2 in August 2019 depicts the broad-leaf forest with trees growing amid a carpet of volcanic rock. Understory vegetation had been cutback.



Figure 17. Photographs depicting various aspects of anthropogenic disturbance at site PH2 and PH1 (bottom left). Slash and burn techniques were used to clear forest habitats, in a practice described locally as 'cleaning the forest'. The effect of this was considered among the most detrimental to habitats and ecosystems that I observed, whereby understory vegetation was removed and burnt in piles. Those fires often spread beyond control across the leaf litter.



Figure 18. Photographs of site PH2 represent the reduction in habitat complexity and vegetation density between sample years. When I mention the removal of understory vegetation, I refer to the near complete stripping of vegetation from the forests interior. For the most part in 2017, slow growing palms (*A. wrightii*) were densely compact throughout site PH2, to the extent that you almost had to 'fight your way through them'. However, by 2019, the forest and palms had been cleared to open up the land for sale and development.

3.1.2: Generating a Disturbance Index (DI)

I regularly visited and monitored the sites during 2018, but could not perform population surveys due to the ongoing activities of land-owners and high-rate of disturbance in the area (i.e. Figure 17); surveys would have not only been biased by the presence of working people, but potentially dangerous owing to disturbance activities. In 2019 when disturbance rate had temporarily ceased, each transect was resurveyed and walked to assess the level of disturbance related impact. Collectively, I considered the sites as exposed to seven forms of disturbance since 2017 (tree felling, understory clearance, palm collection, controlled and uncontrolled fire, rock levelling and human-tourism traffic).

Regrettably, I did not collect any robust environmental or habitat data at the forest sites in 2017, prior to the unanticipated changes I observed. In the absence of that data, I generated a modest disturbance index (DI) to subjectively quantify the factors affecting each site in 2019. Values of 0.5 – 1.5 were given to mark the occurrence of detrimental activities along each transect dependent on severity (minor, medium, major).

Severity of disturbance factors were determined based on quantitative measures where possible, i.e. the number of felled tree stumps (>20cm trunk girth) was tallied for each transect (1-10 cut trees = minor 0.5, 10-20 = medium 1, 20-30 = major 1.5). The same measure was used to quantify the collection of palms, and the number/relative impact of controlled burn-pile patches. The percentage area of each transect affected by fire (uncontrolled) was estimated (0-33% burnt = 0.5 minor, 33-66% = medium 1, 66-99% = major 1.5). Other disturbance classes were difficult to quantify without prior habitat data, so were subject to my own objective comparison. I could not directly measure the amount of understory vegetation lost, human traffic or levelled rock, but I noted their presence and gauged impact based on my observations.

My methods could not account for variance in the severity of impacts caused by any of the disturbance categories, hence they were all weighted with equal effect despite some obvious dissimilarities in potential impact (e.g. the impact of controlled fires were likely to be less than uncontrolled burning). This may have resulted in the under or over classification of some disturbance factors, and hence results from this analysis should be sensibly deliberated.

3.1.3: Visual-Encounter Surveys (VES)

A combination of Capture-Mark-Recapture (CMR), Line Transect (LT) and Distance sampling (DS) methodologies were used to calculate relative abundance and density estimates, as well as gather morphometric data. As described, four forest sites were established, two ca. 9000m^2 survey plots (150 x 60m; PH1 & PH2) and two ca. 6000m^2 plots (100 x 60m; PH3 & IB1). To provide a systematic approach and enable complete survey coverage of these areas, 12 transects were designated, i.e. each site was trisected with three 100 or 150m transects separated by 20m (10 meters perpendicular). Each site contained three transects that were surveyed for three consecutive days, a collective 36 survey occasions across 12 days in both 2017 and 2019.

During each transect, I systematically looked for *A. bicaorum* in all available microhabitats up to 10m perpendicular to the central line, slowly scanning ground-level leaf-litter, logs, volcanic rocks up to understory vegetation and higher towards the canopy layer. Special attention was paid to searching understory palm leaves, tree trunks and branches from 0.5 – 5m high; previously noted as preferred perch substrates for the species (Brown et al. 2017ab). Sounds of movement on the leaf litter were also used to detect *A. bicaorum*. On each transect, I also tallied the presence of other anole species, as well as reptiles considered potential predators or competitors.

Upon encountering anoles, I positioned myself at least 2m away from the individual before recording the distance along and perpendicular to the transect, its body orientation, perch use and current behaviour. With the help of two field assistants, I also measured perch height and diameter, temperature, humidity and wind speed data using a Kestrel weather meter (Model 5500). It took no longer than 2 minutes to record the data per each captured anole in a survey period. After capturing individuals by hand, I promptly contained the individual in a cotton bag, and hung it in the shade until the transect was completed. The bag, anole and original perch of the each anole were numbered, to facilitate the return of individuals to their exact perches post data collection (after being held captive for up to 2 hours). Marking and collecting morphological data on captured anoles was done at the end of each transect, to avoid excessively influencing transect search times and calculations of catch per unit effort (CPUE).

I took morphological measurements using electronic callipers, including snout-vent length (SVL), tail length, and dewlap length. All were measured to the nearest millimetre. Dewlap length was found to be an accurate proxy for dewlap area in *A. lemurinus* (Logan et al. 2012). I followed the method of Logan et al. (2012), measuring the longest distance from the tip of the organ when fully extended to the point where it contacts the chin. The weight of each anole was measured by placing individuals inside a plastic container on a previously calibrated electronic scale, or alternatively by 50g Pesola scale (0.1g accuracy) in its capture bag (deducting the bag weight afterwards). The sex of each anole was visually determined based on dewlap size and the presence or absence of a hemipenal bulge at the base of the tail. Whilst in hand, I also noted any injuries, parasites, the tail status of each individual (complete or broken) and the dewlap colouration. In 2017, captured individuals of suitable size (SVL >50mm) were marked temporarily by suturing one or two 2 mm coloured plastic beads to the base of the tail. As detailed for lizards by Galdino et al. (2005), this method prevented unnecessary recapture and allowed for individual identification on subsequent visits. In 2019, the marking method was simplified to allow for a rapid yet thorough comparison of prior population estimates, instead using non-toxic marker to write an identification number on the anole's dorsum. This method was considered more ethical and appropriate for the purpose of intensive 3-day survey efforts.

3.1.4: Consideration of VES Design and Standardisation

Closed population CMR studies are underpinned by five key assumptions, i.e. 1) each individual (marked or unmarked) has an equal chance of being captured on survey, 2) marking does not affect the individuals chance of survival or recapture, 3) births, deaths, or migration does not occur between capture and recapture surveys, 4) marks are not lost between capture or recapture surveys, and 5) sufficient interval time is allowed between sample occasions for marked individuals to randomly disperse in the population; but not so much time that assumption 1, 3 or 4 are violated (Arnstrup et al. 2006; Alcoy et al. 2013; Anton et al. 2014)

All these assumptions were carefully considered in my survey design; to short or too long a time interval between CMR surveys can violate either set of assumptions, as can the effectiveness of marking and detection. Leaving sufficient time between surveys is essential to enable dispersal of marked individuals, as CMR methods will predict lower population estimates if the probability of them being recaptured is higher relative to unmarked individuals.

To best satisfy the CMR assumptions that the sample population is closed, i.e. that no births, deaths or migration (or the loss of individual marks) occur during the study period; I decided to survey each site for three consecutive survey days whilst rotating transect order and survey time to minimise bias in recapture rates and detectability. I considered a three day survey design short enough to minimise bias generated by loss of markings, unexpected increase, decrease or movement of individuals within the population, but also long enough (c. 24hrs) to allow marked lizards time to randomly intermingle with the unmarked population prior to resampling.

To minimise any additional biasing survey factors, my methods standardised; sampling season and weather; daily period; search area; search time; and quantity and quality of surveyors.

To reduce any bias around the effect of seasonality on anole abundance, all annual surveying commenced during the same dates (July 18 –August 19) and daily period (9:00 – 16:00h), and were only carried out on sunny days; fortunately, no rainy days occurred during any of the consecutive 3-day sampling periods. The starting times and directions of transects were alternated to ensure equivalent sampling conditions across entire survey sites and so that no transect was surveyed disproportionately during the same time of day.

To ensure a consistent search area was maintained, all transects and site boundaries were marked out every 10m using coloured transect tape, and routes were tracked each survey by the same Garmin GPS. Total search time was not restricted to a set limit, but start, end and total time was recorded on every survey to enable a comparison of search effort between transects, sites and years.

As this study took place at KURCF (an NGO that hosts student researchers); the sites were surveyed consistently on each occasion with the help of two additional observers. I acknowledged that limitations in detectability could arise by using different observers on surveys, because people have variable competency levels in locating lizards (Albergoni et al. 2016). To best navigate this effect, all volunteer surveyors were rigorously field-trained to ensure they were familiar with the methodology and competent at locating *A. bicaorum* in its habitat prior to surveys. I remained a constant observer throughout every survey, and was responsible for ensuring all associated anole data was collected in a standardised manner.

Though the method used to mark anoles did change between sample years (i.e. semi-permanent bead-tagging in 2017, to temporary non-toxic marker pen in 2019), it seems unlikely this modification would have had any impact on the comparability of results because site data was collected over a short three-day timeframe and lizards shed relatively infrequently as adults.

After the initial marking in 2017, I was able to opportunistically track three *A. bicaorum* intermittently for periods of up to 12 months, during which I found they occupied a localised territory of c. <10m2 (for the most part perching on a single tree). This demonstrated the beading method was effective for recognising individuals over a time period long enough to speculate on their home range and determine growth rates (see Brown, 2019). With regards to meeting CMR assumptions, firstly, I demonstrated that bead-marks were relatively successful for long-term studies and therefore are unlikely to have been lost during the consecutive three-day sample period of the present study. Secondly, subsequent tracking demonstrated *A. bicaorum* exhibited a high site fidelity, which suggests any confounding CMR effects of immigration or failure to disperse during survey intervals would be negligible, at least in adults with a pre-established territory along my transect routes. Movements of adults within the site was so minimal, I deliberated it possible to treat each transect as a closed-population for CMR analysis without violating movement assumptions. I often recaptured lizards close to their original encounter and release point (the same positions), which I argue relates more so to their territorial nature and pre-existing site fidelity, rather than a failure of the marked individuals to disperse among the population in the allocated c. 24hr interval time between sampling.

3.1.5: Data Analysis

Analysis of survey standardisation and population data comprised various statistical tests, most of which were performed using the software Microsoft Office Excel 2013 and PAST statistical program version 3.25 (Hammer et al. 2001). Prior to selecting appropriate parametric or non-parametric statistical analyses, I determined whether values in my data were normally distributed using a Shapiro-Wilk (S-W) test. As repeat surveys were conducted at the same four sample sites in 2017 and 2019, when comparing annual results in the case of normality, paired two sample or 'repeated-samples' t-tests for equal means were used to determine whether the data collected was consistent or had significantly changed between years. In the case of non-normally distributed data, I used a non-parametric equivalent, i.e. the Wilcoxon signed-rank test for equal medians. I reported *P-values* subject to a Monte-Carlo permutation.

Search effort

Data were displayed by site and year in box and whisker plots. Wilcoxon signed-rank tests were used to analyse annual differences in the total survey times recorded for each transect, in order to determine whether survey effort (in minutes) was standardised between years. To better account for search effort and enable a comparison of sites that had transects of different set lengths (i.e. 100 or 150 m), the same analysis was also performed on search speed (meters walked per minute), which was calculated using a simple metric, i.e. dividing the distance walked (transect length - meters) by the total time spent (survey time - minutes).

Catch per-unit effort (CPUE)

To determine catch per-unit effort (CPUE), I isolated encounter data (including recaptures and missed) for each transect and survey occasion, as well as the total search time spent on each survey. I then calculated the CPUE (total animals observed / search time) in minutes for each site and individual transect performed. CPUE (anoles per minute) was converted to CPUE (anoles per hour) by multiplying by 60. Wilcoxon signed-rank test were used to determine whether any significant changes in CPUE had occurred between sample years; data displayed in a box plot.

Detectability and recapture rate

To assess whether anole detectability had remained consistent throughout my study, I calculated the percentage recapture rate for males and females across all sites during both years. I combined the annual site data for both sexes separately, and used a paired sample t-test to determine whether there was significant differences in the mean recapture rates of males and females. Because recapture rates appeared similar for both sexes, I combined male-female site data by year and used a paired sample t-test to investigate whether overall *A. bicaorum* recapture rates had changed between years. Data was visualised in a bar chart.

Relative Abundance

Using CMR data, annual abundance estimates for each site and transect were calculated using the Lincoln-Peterson and Schnabel Index equations (e.g. Alcoy, 2013). A formula sheet was generated in Excel 2016 to compute standard equations for population estimates using data collected during two survey occasions (Lincoln Index) and three survey occasions (Schnabel index), see Figure 19.

Lincoln-Peterson Index:

$$N = \frac{M + C}{R}$$

N = Estimation of Population Size

M = Captured, Marked and Released (1st Sample)

C = Total Captured (2nd Sample)

R = Total Marked Individuals Recaptured (2nd Sample)

Schnabel Index:

$$N = \frac{\sum_{i=1}^{M} M_i C_i}{\sum_{i=1}^{M} R_i}$$

N = Estimation of Population Size

Mi = the total number of previously marked animals at time *i*

Ci = the number caught at time *i*

Ri = the number of marked animals caught at time *i*

Figure 19. A simplified equation for the Lincoln-Peterson Index (estimate population size based on two sample occasions) and an algebraic equation for the Schnabel Index (estimate population size based on a series of three or more sample occasions). As by Alcoy (2013).

Lincoln Index methods assume the proportion of marked individuals recaptured in the second sample represents the proportion of marked individuals in the population as a whole (Amstrup et al. 2006). Schnabel index estimates are in essence weighted averages and a continuation of the Lincoln Index to incorporate three or more survey occasions (Anton et al. 2014). Both can be used to generate CMR results from closed populations (see 3.1.4), which assumes that the population does not change in size during the study period, whereby the effects of births, deaths, and migration are negligible (Kendall, 1999).

Each site was initially analysed as a whole, combining the daily survey results (Captured, New and Recaptured anoles) of the three transects composing each site, to obtain two and three

consecutive day estimations using the Lincoln and Schnabel Index. The same CMR analysis was then performed on each transect independently. This enabled me to examine variation within, as well as between sites. The presented values were rounded to the nearest integer. The results of both the Lincoln and Schnabel index were plotted in bar charts to visualise results. To advise future research and select the most appropriate relative abundance estimator for my study, I compared the results of both the Lincoln and Schnabel index using a Wilcoxon signed-rank test to identify whether they yielded significantly different estimates. The Schnabel Index estimates were then analysed using ANOVA to test whether annual populations along transects within each site varied significantly, and paired t-test were used to conclude whether transects had collectively maintained their abundance, declined, or increased between years.

Disturbance index

The percentage difference of the annual transect abundance estimates (Schnabel Index) were regressed against a numeric rating of disturbance level (see 3.1.2), to identify whether declines in *A. bicaorum* abundance correlated with quantifiably subjective measures of habitat degradation. I used an Ordinary Least-squares (OLS) regression model to plot the line of best fit and test for a significant correlation in the data. OLS estimate the parameter of a linear regression model and minimize the sum of the squared errors (i.e. the difference between observed and predicted values). This was used to identify the strength in the relationship between percentage difference in relative abundance (a dependent continuous response variable) and disturbance level (independent explanatory variable).

Relative Density

A density index was generated by dividing the number of anoles captured by the area searched. I estimated a range of potential densities at each transect to encompass the potential variation in anole density. To estimate the minimum number of *A. bicaorum*, the total individual anoles observed during each survey (excluding missed and recaptures) was divided by the area of each transect; To provide a density estimate, I used the population size estimations of the Schnabel index to provide an upper relative range limit, given the estimations were always greater than the raw capture data. All values were rounded to the nearest whole number. Paired t-tests were used to test for significant changes in both the relative and raw annual transect density estimates. Percentage difference in relative density estimates were also tested for significant correlations against disturbance level using OLS regression.

Distance Sampling

To ensure the observed patterns in relative abundance and density indexes were robust to different methods, I used the software DISTANCE 7.3 (Thomas et al. 2010) to analyse the distance-sampling data from CMR line transects. Unlike CMR based index calculations that assume no relationship between detection and distance, the DISTANCE program uses model-fitting algorithms to generate a detection function that is based on the proportion of all individuals located along the transect and their perpendicular distances from the transect line. This function can be used to extrapolate the population densities of each transect to a given area of suitable habitat, because it accounts for variance in detection probability. Distance sampling assumes that every individual directly along the transect line is detected, and that detectability of individuals decreases with their perpendicular distance away from the line (Buckland et al. 1993). The relationship of distance and detectability must be considered when estimating population densities from line transects, as it infers numerous key assumptions necessary to generate robust absolute population estimates (Buckland et al. 2001; 2015). The four key assumptions of distance sampling are, 1) Transects are located randomly and animals are independently distributed; 2) The probability of detecting an animal directly on the transect line is 100% (g (0)=1); 3) perpendicular distances to the transect are measured accurately; 4) surveys represent a snapshot in time where animals do not move (Buckland et al. 2001).

All observations (including recaptures) and sample information on age and sex were incorporated into trialled distance models by post-stratification (Thomas et al. 2010). Density was calculated in anoles per hectare (D). To enable extrapolation of results and estimation of total abundance (N), the region area was set to the available c. 3.45km^2 of forest habitat on Utila (as predicted by Maryon, 2020).

To conclude the best results from my data, I trialled and compared numerous models for detection function. The Akaike's Information Criteria (AIC— Akaike, 1973) was used to determine the model that best suited the data (Buckland et al. 2001; 2015). The AIC selection method maximises the robustness of results while minimizing bias and variance when adding model parameters. My analysis identified a hazard-rate key function with cosine adjustments post stratified with Sex (M/F) as the most appropriate model; that ran without errors. Separate models that produced density estimates (post stratified by age class and sample site) were discounted as they ran with numerous warnings, and did not produce robust AIC values, or meet the models Chi^2 goodness of fit requirements (Table 2).

Table 2. A list of models that were trialled for both 2017 & 2019 data prior to truncation. All models were ran with hazard-rate key function and cosine adjustments, as automatically selected by DISTANCE when trialling different detection functions. The tests varied in that estimates were post stratified by either sex, age class or sampling site. Based on the lower AIC value, models that post stratified results by sex were selected for each year. Key: Number of parameters (# P); Effective Strip Width in meters (ESW); 95% Confidence Intervals (95% Conf. Interval - Lower & Upper Limits); Density of individuals analytic coefficient of variance (D CV).

Model	*Delta AIC*	*AIC value*	*ESW*	*Density*	*95% Conf. Interval*		*D CV*
2017 - by sex	**0**	**1552.94**	**1.67**	**279**	**176**	**444**	**0.239**
2017 – by age	20.53	1573.47	1.66	245	164	365	0.205
2017 – by site	205.24	1758.18	1.54	289	205	403	0.172
2019 – by sex	**0**	**852.19**	**1.97**	**127**	**78**	**209**	**0.255**
2019 – by age	79.75	931.94	1.86	147	87	247	0.269
2019 – by site	79.75	931.94	1.86	147	85	254	0.279

Because initial models gave a detection likelihood of c. 10% at 10 m perpendicular to the transect line, I reduced biases on distance-detection probability by applying a right truncation on my dataset. Truncation was especially necessary because during 2019, there was an apparent increase in individuals spotted from greater distance, which violated distance-detection assumptions by implying a greater portion of individuals closer to the transect line had been missed. Rather than anoles being missed, the 2019 detection bias probably occurred due to the effect of understory clearance on increased visibility at 3/4 sites (i.e. more anoles were located at 10m from the transect, as appose to from 6-9m).

I assessed the results using different right truncation to discard observations after 5, 6, 7, 8 and 9 meters. The resulting density estimates did not vary substantially, but on assessment, a six meter truncation was considered to capture the most data whilst retaining non-significant Chi^2 goodness of fit, high detection probability and the lowest AIC and CV value. Buckland *et al.* (2001) suggest truncating the data where the probability of detection is around 0.15. I therefore chose a 6 m truncation and applied it to both datasets to enable an appropriate comparison between annual estimates. A two tailed z-test tested for significant differences between the mean annual density estimates (Buckland et al. 2001; Anderson et al. 2013).

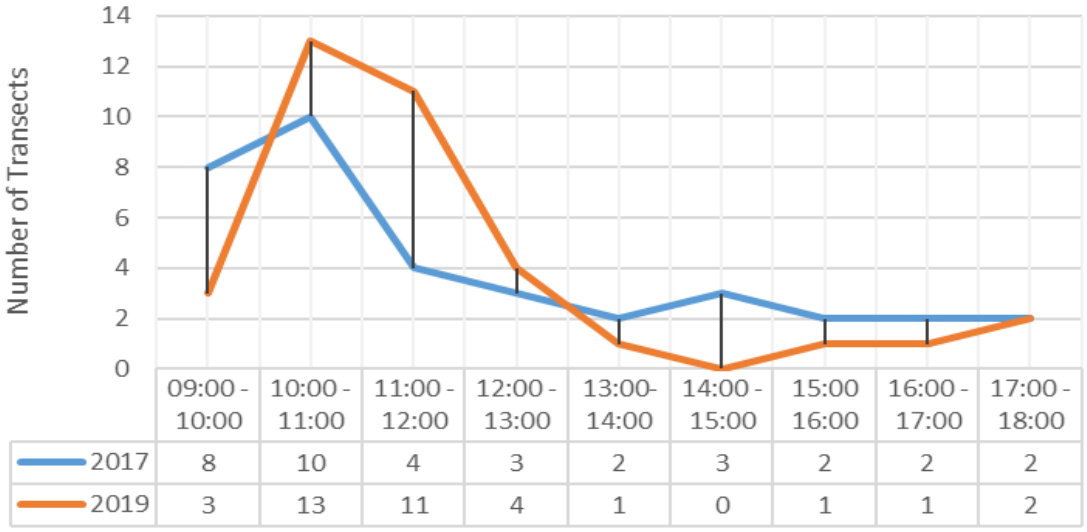
3.2. Results

Between the dates of July 18 and August 19 2017, a total of 36 surveys were conducted along 12 transect lines at four sites (3 transects x 3 daily occasions per site). The study made a total of 521 *A. bicaorum* observations in 1971 minutes of active searching. Of these observations, 47 anoles were 'missed' (not captured) and hence disregarded from CMR analysis. Following this adjustment, we report CMR data as 474 encounters of 332 individual *A. bicaorum* and 142 recaptures. The overall recapture rate was 43%. Of those captured, morphometric data was collected for 133 males and 121 females.

On the same dates in 2019, the four sites were resurveyed and a total 253 observations were collated in 1719 minutes spent on transects. Of these, 24 missed observations are removed from CMR analysis. This resulted in 229 observations of 168 marked individuals (61 recaptures; 36% rate), with morphometric data collected for 59 males and 74 females. Across the 36 annual survey occasions, the mean number of *A. bicaorum* detected on a given transect in 2017 was 13.2 (n= 474 total anoles; std.dev = 9.1), dropping to 6.4 (n = 229 total anoles; std. dev = 2.9) in 2019, a decline of 53%.

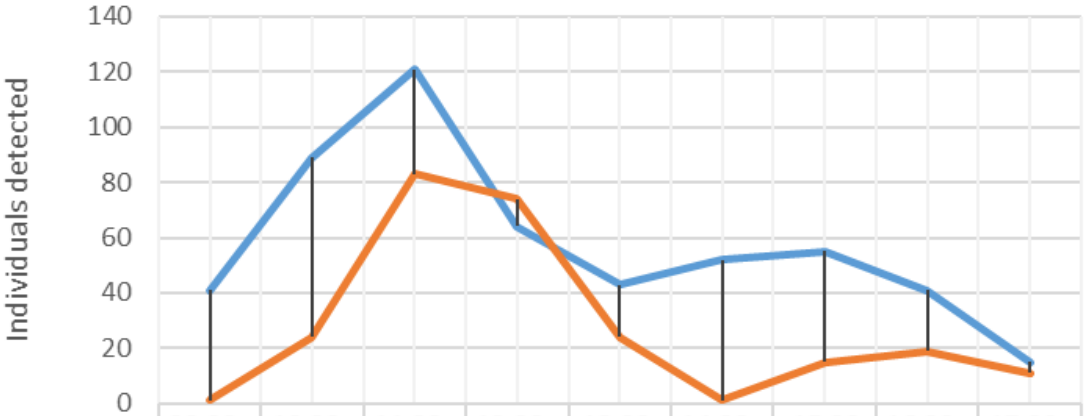
In both years, c. 90% of the anoles detected on survey were successfully captured by hand. Only those captured or identified by their marks on subsequent occasions are included in the CMR analysis, which includes new individuals encountered but not captured on the final survey occasion. The majority (68%) of the transects surveyed in 2017 and 2019 commenced between 09:00-13:00h; 64% of anoles were caught between those hours (Figure 20 & 21).

Transect start times, shown in Figure 20, indicate more survey effort occurred during the afternoons of 2017, likely because a generally higher anole abundance meant each transect (and post-measurement session) took longer to complete. Surveys in 2017 started mostly from 9-11am, whereas in 2019 most started between 10-12am. Encounter rates in 2019 were lower despite having more transects start during the period of peak anole activity in 2017. Encounter times in 2017 (Figure 21) suggest peak encounter periods are concentrated between the hours of 10:00 – 13:00 irrespective of survey start times. Lizard captures were higher at this time during 2017, despite more transects starting during that period in 2019, suggesting a decline in abundance. Independent of search time, I usually found individuals could be located throughout the day in appropriately shaded habitat.



	09:00 - 10:00	10:00 - 11:00	11:00 - 12:00	12:00 - 13:00	13:00- 14:00	14:00 - 15:00	15:00 16:00	16:00 - 17:00	17:00 - 18:00
2017	8	10	4	3	2	3	2	2	2
2019	3	13	11	4	1	0	1	1	2

Figure 20. The start times of 36 transects conducted in 2017 & 2019. Transects were rotated and conducted throughout the same daily periods that coincide with peak anole activity times (10:00-13:00h).



	09:00 - 10:00	10:00 - 11:00	11:00 - 12:00	12:00 - 13:00	13:00- 14:00	14:00 - 15:00	15:00 16:00	16:00 - 17:00	17:00 - 18:00
2017	41	89	121	64	43	52	55	41	15
2019	1	24	83	74	24	1	15	19	11

Figure 21. The number of *A. bicaorum* detected on transect in association with time of day. Including those missed, a total 521 anoles were detected in 2017, and 252 in 2019.

3.2.1: Quantifying Search Effort (Survey Time and Speed)

Transects were walked at a steady pace and the time from start to finish was recorded in minutes. As I did not set a time limit for each search occasion (e.g. 1 hour searching per transect), effort was not entirely standardised among all surveys. However, search efforts were consistent between years. Table 3 (Appendix 1) shows a breakdown of the time spent surveying each transect and site. In 2017, a total of 1971 minutes were spent walking transects, compared to 1719 minutes spent in 2019. Figure 22 shows this data plotted in a Box and Jitter plot. On average, I spent seven minutes extra surveying each transect in 2017 (μ 54.75 mins) than in 2019 (μ 47.75). Search times for both years tested significantly non-normal using a Shapiro-Wilk test (N = 36, S-W = 0.87 [2017]; 0.90 [2019], P = <**0.05**). However, a Wilcoxon signed-rank test found there was no significant difference in the median of 36 transect survey times between years (N = 36, W = 405, z = 1.132, P = >0.05). Reductions of search time in 2019 only occurred on 50% of transects (18/36). These small differences in survey times are unlikely to have significantly influenced population estimates, especially because the primary reason for some shorter survey times is due to less handling time in 2019.

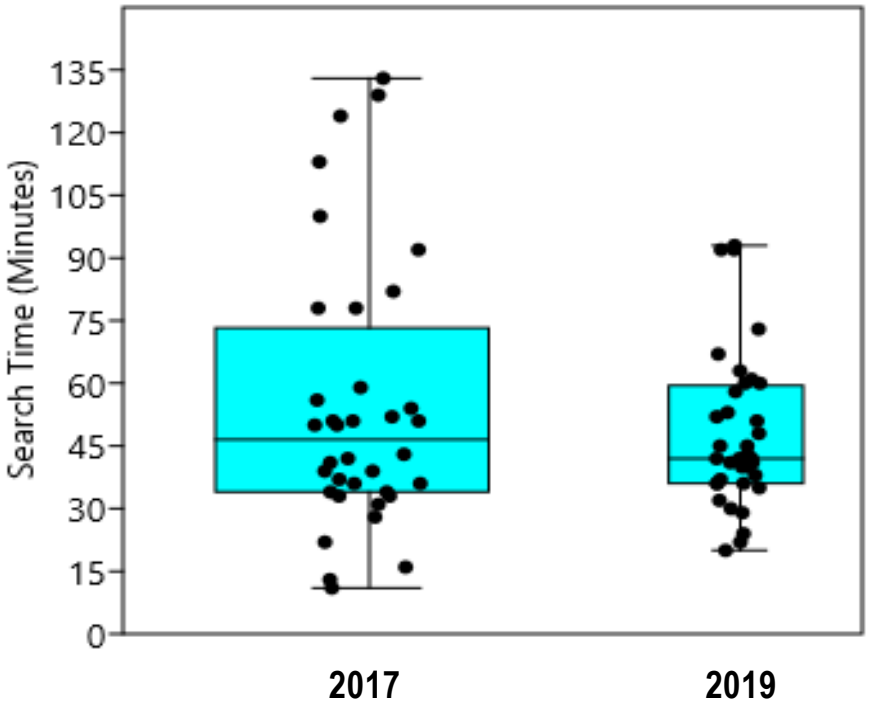


Figure 22. The total search times of 36 transects completed in 2017 and 2019 were consistent between years; (P = >0.05).

Because I had surveyed transects of two set lengths (100m or 150m), I also compared the speed in which transects were completed between years. I calculated survey speed in meters per minute (Table 4 - Appendix 1). Transects across all sites were walked on average at μ 2.97 (±0.35) m/min in 2017, and μ 3.18 (±0.18) m/min in 2019 (μ difference of 0.21m per minute – Figure 23). A Shapiro-Wilk test demonstrated that search speed in 2017 was significantly non-normal (N =36, S-W = 0.822, *P* = <**0.05**), whereas in 2019 it was uniform (N =36, W = 0.975, *P* = >0.05). Using a Wilcoxon signed-rank test, I found no significant difference in the medians of annual search speed (N = 36, W = 343, *z* = 0.157, *P* = >0.05).

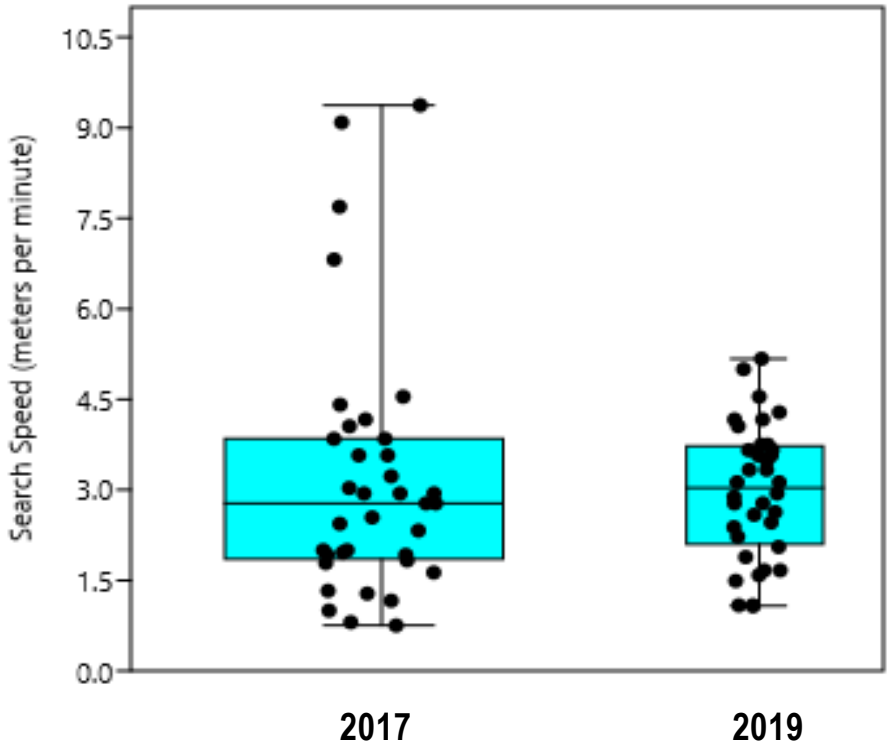


Figure 23. Transect search speeds (meters per minute) were consistent between both sample years (2017 and 2019); (*P* = >0.05).

While no significant differences were identified in the transect time and speed between sample years, the slight reduction in mean 2019 search time and increase in 2019 survey speed may be attributable to changes in anole abundance and environmental factors at each site.

Three of four sites (PH1, PH2, IB1) had been subject to substantial disturbance and some transects had been essentially gutted of their forest interiors since the original sampling occasion. In my opinion, the clearance of dense understory vegetation had numerous inadvertent effects on effort and the total time needed to complete a transect; 1) It reduced search times by making it easier to walk through the forest (less obstacles and clambering); 2) cleared understories improved anole visibility and detectability over a greater distance; 3) reduced complexity of vegetation meant that there was simply less structures to scan for the presence of anoles. Another consideration is that I apparently encountered less anoles, that reduced the effect of artificial inflation on survey times from transect data collection. While I minimised any search time bias by collecting the bulk of anole data once the transect was completed, it still took approximately 1-2 minutes processing time per anole (i.e. to capture and record positioning/microclimate). On transects with many anoles, this accumulation of brief pauses might of incurred lengthy added periods to total survey time and calculations of search speed.

3.2.2: Catch per Unit Effort (CPUE)

Overall, a 44% reduction in CPUE occurred across sampled sites from 2017 – 2019 (Figure 24). Site IB1 CPUE dropped from 16.2 *A. bicaorum* per hour to 10.9, PH1 from 23.4 to 11.3, PH2 from 16.8 to 8.1, and lastly PH3 from 5.5 to 4.4. Table 5 presents the transect data for total anoles captured within search times across the three-day sample periods. Considerable reductions in CPUE were identified in all but one transect (PH3 T3), because it yielded no anoles in 2017. Shapiro-Wilk test found CPUE in 2017 was significantly non-normal (N = 36, S-W = 0.916, P = <0.05), but that CPUE in 2019 was normally distributed (W = 0.950, P = >0.05). A Wilcoxon signed-rank test was used to analyse the median CPUE of 36 individual annual transect occasions in 2017 (median – 0.27) and 2019 (0.12), which detected a significant decline between years (difference = 0.15, W = 551, P = <**0.001**).

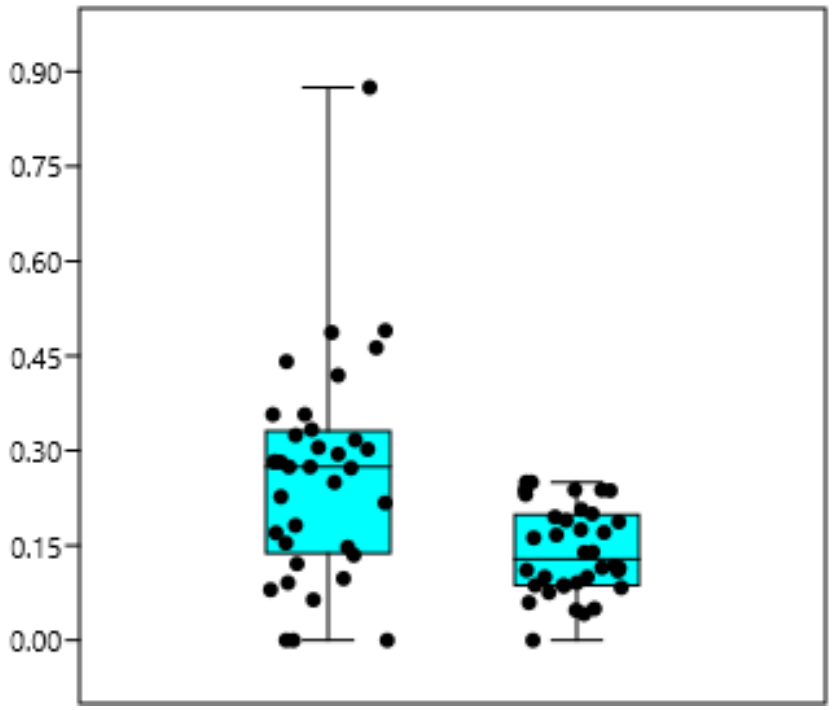


Figure 24. A comparison of Catch per-Unit Effort (anoles per minute) along transects between sample years; (*P* = <**0.001**)

Table 5. Catch per Unit Effort (CPUE) calculated using the total encounters (N)/total search time for each transect. Reductions in CPUE during 2019 transect surveys are highlighted in bold.

		2017				***2019***			
Site	*Transect*	Total Time	N	CPUE (minute)	CPUE (hour)	Total Time	#N	CPUE (minute)	CPUE (hour)
	T1	87	41	0.47	28	170	29	**0.17**	**10**
PH1	T2	144	58	0.40	24	125	27	**0.22**	**13**
	T3	222	78	0.35	21	107	20	**0.19**	**11**
	T1	94	25	0.27	15	111	10	**0.09**	**5**
PH2	T2	**250**	**72**	0.29	17	152	20	**0.13**	**8**
	T3	210	58	0.28	16	149	26	**0.17**	**10**
	T1	357	45	0.13	7	277	24	**0.09**	**5**
PH3	T2	180	15	0.08	5	190	13	**0.07**	**4**
	T3	127	0	0.00	0	158	9	0.06	3
	T1	132	39	0.30	18	114	24	**0.21**	**12**
IB1	T2	110	34	0.31	19	100	22	**0.22**	**13**
	T3	58	8	0.14	8	66	5	**0.08**	**4**

3.2.3: Detectability and Recapture probability

The results of transect surveys (3 transects x 3 days per site), i.e. total captures, recaptures and new individuals are shown in (Table 6 – Appendix). I computed the percentage recapture rate of both sexes in 2017 and 2019 (Table 7 - Appendix); recapture rates varied among sites both years from 0.33 – 0.83 in males, and 0.13 - 0.92 in females. Smaller values represent sites with a high amount of new individuals and lower rate of recapture, indicating a large intermixing population with a lower rate of detectability.

As data proved to be distributed normally (N = 8, S-W = 0.887 [2017]; 0.985 [2019], P = >0.05), I used a paired sample t-test to test whether significant differences were present in the mean recapture rates of males and females (all sites/years). There was no significant difference in the mean annual percent recapture rates of males (μ 0.53) and females (μ 0.52), (μ difference = 0.01, 95% conf. -0.166 0.184, t = 0.12, P = >0.05).

Given approximately 50% of all captured anoles (males and females) were recaptured at least once, it is likely my study satisfied the CMR assumption that both marked and unmarked individuals of both sexes have an overall equal chance of being captured relative to any difference in the ability to detect them between sites (Figure 25).

I then combined male-female site data by year to determine changes in *A. bicaorum* recapture rate; both years were normally distributed (N = 8, S-W = 0.861 [2017], 0.832 [2019], P = >0.05). A paired sample t-test determined there was no significant difference in the 2017 (μ 0.58) vs 2019 (μ 0.47) mean site recapture rates (μ difference = 0.11, 95% conf. -0.094 0.311, t = 1.27, P = >0.05).

Importantly, those results demonstrate that on average, the percentage *A. bicaorum* recapture rates were near equal in 2017 and 2019. This suggests that despite any changes in anole habitat, disturbance level, search effort or abundance, my rate of detection was relatively consistent and I sampled a constant proportion of the population during both survey years. My overall results on detectability and recapture rate meet key assumpions and suggest my CMR analysis will reflect a comparably representative population estimate for both survey years (Figure 26).

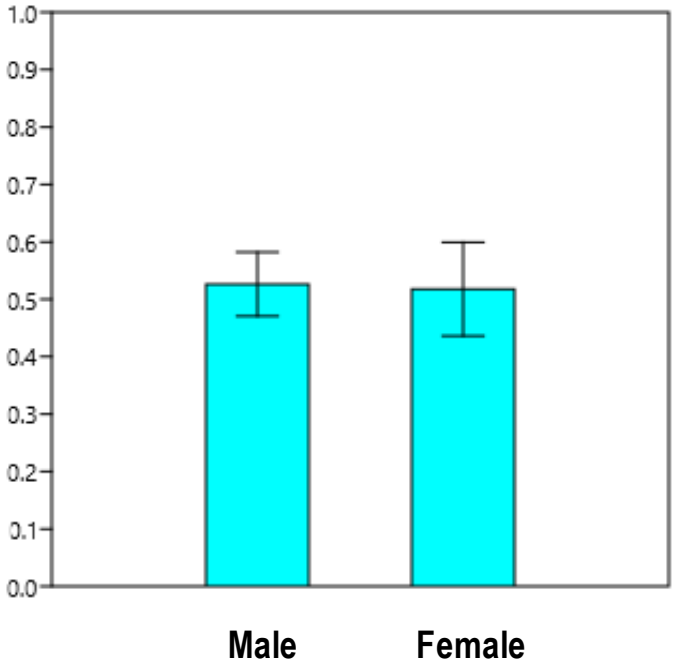


Figure 25. The percentage recapture rate of males vs females using combined annual data (2017 & 2019). Mean recapture rate was 0.1 higher in males, but not significantly: (*P* = >0.05).

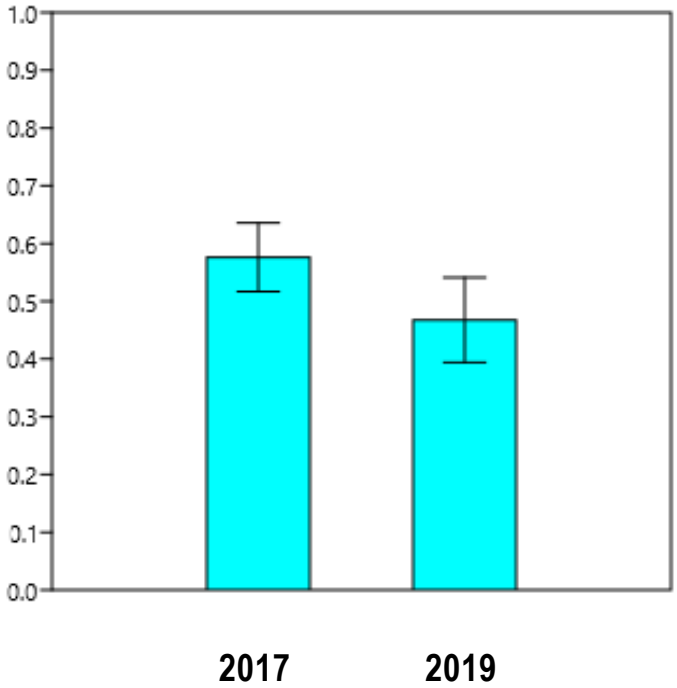


Figure 26. The percentage recapture rates of *A. bicaorum* (males & females combined) for 2017 vs 2019. Mean percent recapture was greater in 2017 than in 2019, but not significantly different: (*P* = >0.05).

3.2.4: Relative Abundance Estimates

Population estimates for sites in 2017 and 2019 generated by the Lincoln index and Schnabel index are compared in bar charts; calculated by site (Figure 27 & 28) and individual transects (Figure 29 & 30).

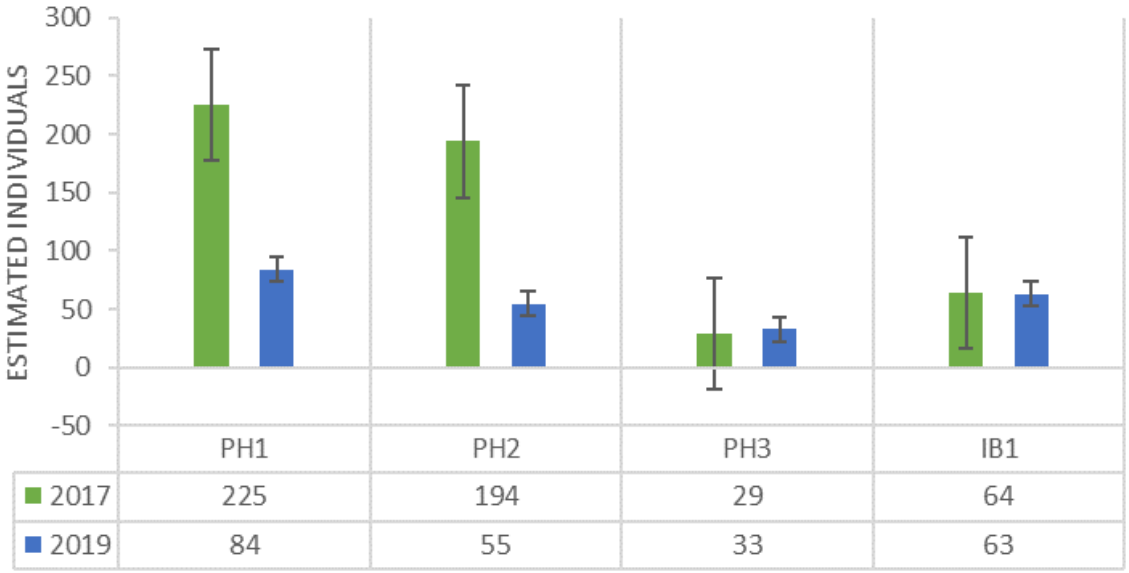


Figure 27. A comparison of 2017 & 2019 Lincoln Index population estimates for *A. bicaorum* across the four sites (including standard error bars).

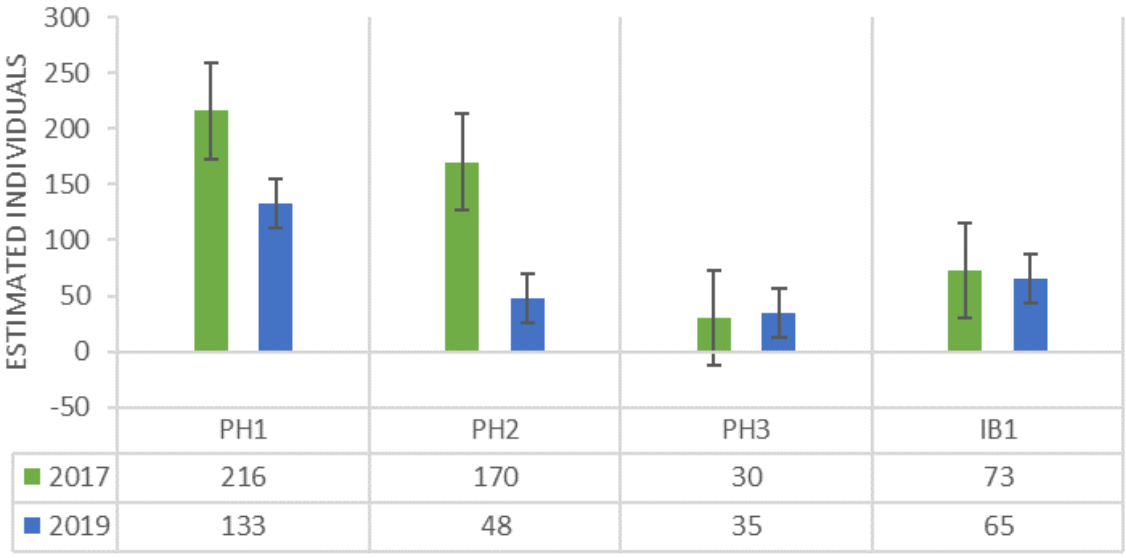


Figure 28. A comparison of 2017 & 2019 population estimates generated by the Schnabel Index for *A. bicaorum* across the four sites (including standard error bars).

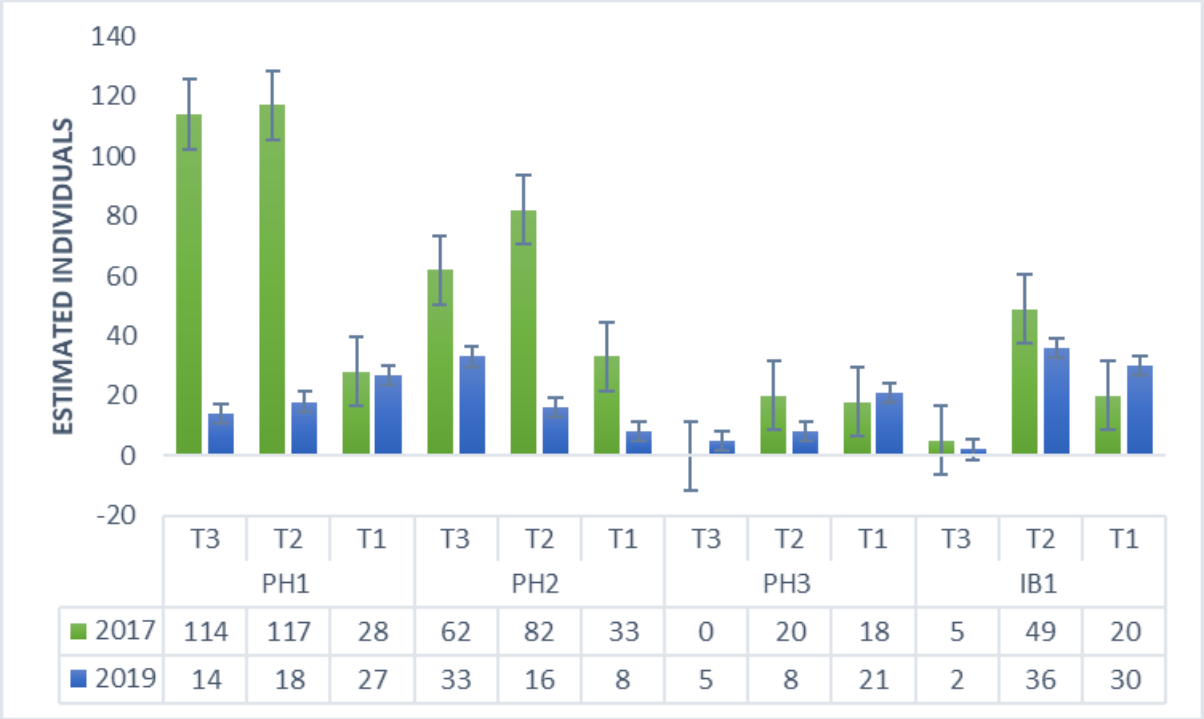


Figure 29. The 2017 & 2019 Lincoln Index population estimates of *A. bicaorum* on the 12 transects within the four sites (including standard error bars).

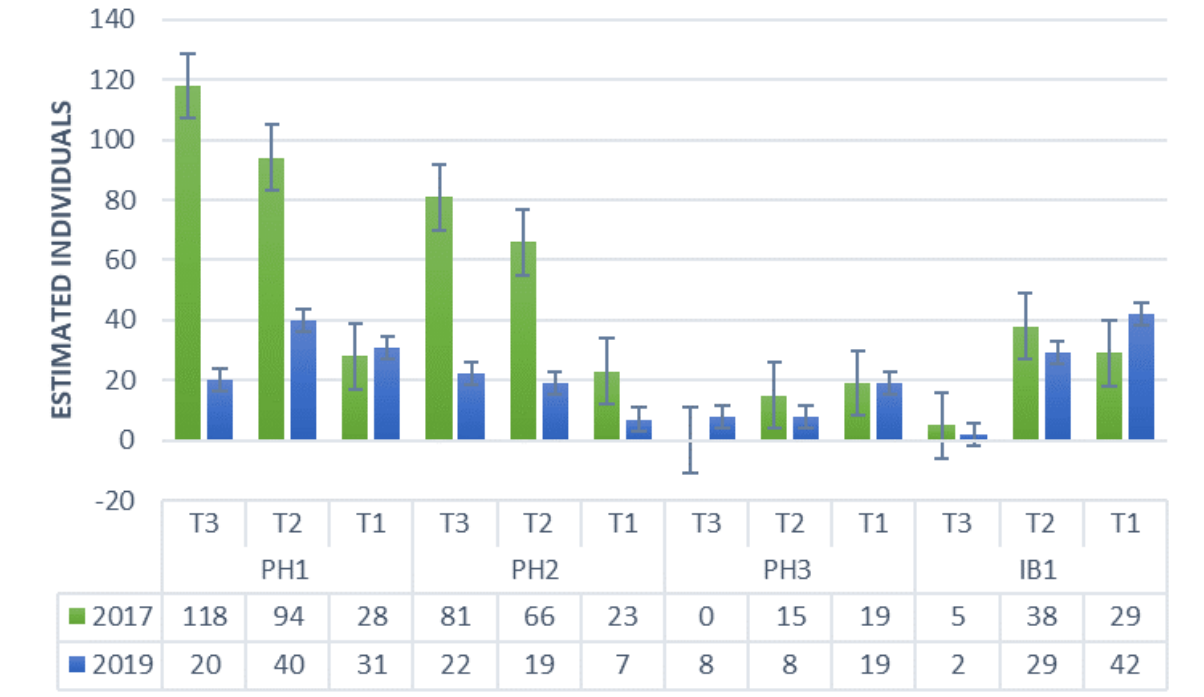


Figure 30. The 2017 & 2019 Schnabel Index estimates of *A. bicaorum* populations on the 12 transects within the four sites (including standard error bars).

Comparison of estimates from CMR indices

As I used two different albeit similar index equations to generate abundance estimates, I first compared those results. The 8 site estimates generated by Lincoln index estimates in 2017 and 2019 had non-normal distribution (N = 8, S-W = 0.791, P = <**0.05**), whereas Schnabel index were normally distributed (W = 0.879, P = >0.05). For both methods, the 2017 & 2019 annual transect estimates combined tested significantly non-normal (N = 24, S-W = 0.791 [2017]; 0.824 [2019]. P = <**0.05**). Assuming non-normality, a Wilcoxon signed-rank test analysed the difference between the medians (m) of pooled annual site estimates using either method (n = 8, Lincoln Index (m 63.5), Schnabel Index (m 69), m difference = 5.5, W = 19.5, z = 0.211, P = >0.05), and the transect estimates of both years (n = 24, Lincoln index (m 20.5), Schnabel index (m 22.5), m difference = 2, W = 96.5, z = 0.06, P = >0.05).

Unexpectedly, I detected no significant difference in the abundance estimates produced by either the Lincoln or Schnabel index methods, demonstrating from a conservation management perspective in this case, both two and three consecutive day sample efforts produced comparable results. Opposite to as expected (i.e. that the Lincoln index may inflate estimates – Anton et al. 2014), overall, the Schnabel index produced site and transect estimates on average 8.7 - 9.8% greater than the Lincoln Index, but this difference was insignificant.

The similarities in the combined site and transect estimates generated by both methods are visualised in a box plot (Figure 31). Similarities may derive from the fact I used two and three consecutive day sampling, only leaving a short 24hr interval between surveys. Nonetheless, I believe this finding indicates I sampled a constant proportion of the population per survey and thereby attests to the robustness of my abundance estimates. My findings concerning the reliability of the Lincoln index may help optimise the planning of future studies, in as much that a third of the total time spent surveying transects could have been reallocated (e.g. to create additional survey sites) whilst still producing a dependable estimate. This may benefit future studies that have a small sampling window, limited access to a remote field sites or that plan on obtaining rapid population estimates from sites at more regular intervals. Wherever possible however, I acknowledge that supplementary sample occasions are irrefutably beneficial in substantiating the reliability of estimates (Amstrup et al. 2006). For that reason, I have chosen to only use abundance estimates produced by the Schnabel index in my results herein.

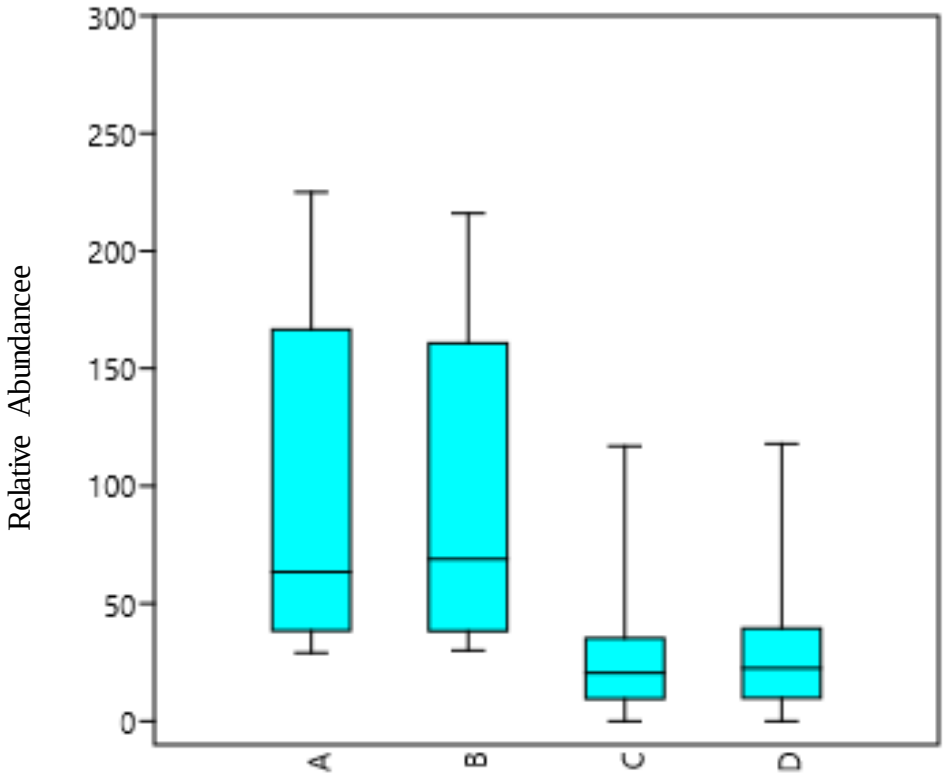


Figure 31. Comparison of Lincoln and Schnabel Index relative abundance estimates. Separately, site and transect estimates for 2017 and 2019 were combined; Lincoln index (A = sites, C = transects) and Schnabel index (B = sites, D = transects). No significant differences were detected among site and transect estimates using either method (P = >0.05), but Schnabel index produced on average greater estimates.

The Schnabel index analysis of 2017 site data provides a broad overview of *A. bicaorum* populations prior to substantial change, and identifies a difference in the abundance of anoles within each forest habitat. In Figure 28, population estimates across sites ranged widely from 30 – 216 individuals in 2017. Estimations for site PH1 and PH2 (the sites most similar in forest composition) are >50% higher than those of sites IB1 and PH3, and IB1 estimates are c. 50% greater than PH3, even though survey area at PH1 and PH2 was only 33% larger than IB1 and PH3. As site PH3 was a semi-disturbed and somewhat degraded coastal habitat prior to my sampling in 2017, the resulting lower abundance estimates are not so surprising, given it appeared to have the least trees of any site.

In Figure 30, Schnabel index estimates varied between transects at any given site, but they differed more between sites than they did among themselves. Transects T2 & T3 at sites PH1 and PH2 were most comparable for high abundance, indicating those palm-dominated hardwood forests have a high suitability for *A. bicaorum*. Transects at PH3 yielded the lowest estimates, which suggests that the semi-degraded quality of this coastal forest was not appropriate for high-density populations.

An ANOVA found no significant difference between the mean transect estimates of each site in 2017 (df = 3, F = 3.55, P = 0.067), suggesting that annual variance within sites was minimal (Figure 30). However, such a small sample set did not hold much statistical power and may be subject to a false negative type II error; the p-value was within 0.02 to α-level of <0.05, and prior to a Bonferroni correction, a Dunn Post-hoc analysis would identify significantly lower abundance at site PH3 than PH1 and PH2 (P = **<0.05**). This contrasts the ANOVA on 2019 estimates that yields a non-significant result with much stronger confidence limits (df = 3, F = 0.46, P = >0.7), implying there was less variation in abundance among 2019 than 2017 sites.

3.2.5: Disturbance-driven trends in relative abundance

Since I collected the primary anole dataset in 2017, land-use change and an increase in disturbance occurred in the eastern region. As of 2019, all the sample sites were impacted differently by anthropogenic activities. Comparing 2017 and 2019 CMR data using the Schnabel Index shows a decline in the estimated population size of 3 out of 4 sites. As in Figure 28, estimated population size decreased overall by c. -38% at site PH1; -72% at site PH2 and -11% at site IB1. Only site PH3 indicated a +17% increase in estimated population size; however, equal numbers (29 individuals) were caught at PH3 in both sample years (Table 6 - Appendix). In Figure 30, declines in estimated population size can be seen in 8/12 (66%) of transects. The sharpest declines occurred on transects at site PH1 and PH2.

Schnabel index estimates for both years were normally distributed (N = 12, S-W = 0.9 [2017], 0.94 [2019], P = >0.05). I therefore used a paired sample t-test to determine significant differences in the mean of population estimates between years. The mean estimated population size of 12 transects in 2019 was 20.6; significantly lower than the 2017 mean estimate of 43 (μ difference = 22.4, 95% conf. = 0.7 44, t = 2.2749, P = <**0.05**). Overall, the mean of annual population estimates decreased significantly by c. 52% from 2017-2019.

To identify whether *A. bicaorum* decline was linked to rising disturbance, in the absence of physical habitat data, a basic disturbance index (DI) was used to generate a rating for each transect to quantify disturbance level. Scores of 0.5 (minor), 1 (medium), 1.5 (major) were designated to represent the severity to which each transect had been impacted by seven separate forms of disturbance (Table 8).

Table 8. A basic disturbance index (DI) classifies factors affecting at each site. Values of 0.5 – 1.5 was given to mark the occurrence of detrimental activities along each transect dependent on severity (minor, medium, major); as defined in methods. Disturbance classes as follow - Tree felling (TF); Understory Clearance (UC); Palm Collection (PC); Controlled Burning (CB); Uncontrolled Burning (UB); Rock Levelling (RL); Human Traffic (HT). A higher DI value should equate to a higher level of disturbance.

Site	***Transect***	***TF***	***UC***	***PC***	***CB***	***UB***	***RL***	***HT***	***DI***
PH1	1			0.5				1.5	**2**
	2	0.5	0.5	0.5		1.5		0.5	**3.5**
	3	0.5	1.5	1	1	1.5		1	**6.5**
PH2	1	1.5	1.5	1.5	1		1.5	1	**8**
	2	1.5	1.5	1.5	1	0.5	1		**7**
	3	1.5	1.5	1	1		0.5		**5.5**
PH3	1	1			0.5			1	**2.5**
	2	1	0.5		0.5			1.5	**3.5**
	3	0.5						1.5	**2**
IB1	1	0.5	1						**1.5**
	2	0.5	1.5	1.5					**3.5**
	3	0.5	1			1.5		1	**4**

I compiled the disturbance index ratings and results of the 2017 and 2019 Schnabel index estimates by site and transect. To test for a correlation relative to the population index for that sampling unit, I calculated the percentage difference between 2017 and 2019 relative abundance (Schnabel index) estimates (Table 9).

Table 9. Schnabel index population estimates for each individual transect (2017 & 2019); ordered alongside the designated disturbance index value (Table 8) and the calculated difference between annual estimates (change in population size). Percentage change in relative abundance given in brackets.

Site	*Transect*	*2017 Estimate*	*2019 Estimate*	*Disturbance Index (DI)*	*Estimate Difference*
PH1	1	28	31	2	3 (+10.7%)
	2	94	40	3.5	54 (-57.5%)
	3	118	20	6.5	98 (-83.1%)
PH2	1	23	7	8	16 (-69.6%)
	2	66	19	7	47 (-71.2%)
	3	81	22	5.5	59 (-72.8%)
PH3	1	19	19	2.5	0 (0%)
	2	15	8	3.5	7 (-46.6%)
	3	0	8	2	8 (∞)
IB1	1	29	42	1.5	13 (+44.8%)
	2	38	29	3.5	9 (-23.6%)
	3	5	2	4	3 (-60%)

An Ordinary least square (OLS) regression model was used to identify the 'line of best fit' to compare the DI ratings against the percentage difference in relative abundance for transects at each site (Table 9; Figure 32). Percentage change was normally distributed (N 11, S-W 0.881, $P = 0.1$), as were residuals of both data (Std. E = 26.7); no positive autocorrelation was detected using the Durbin Watson (DW = 2.1, $P = >0.05$), or heteroscedasticity via the Bruesch-Pagan statistic (BP = 2.2, P (homoscedastic) >0.05). The OLS regression identified that percentage decline in relative abundance correlated significantly with disturbance level (Slope a:-14.33, Std. error a: 4.3957, t:3.26, Intercept b: 19, Std. error b: 19.9, P (slope) <**0.01**; 95% bootstrapped confidence intervals (N=1999): Slope a: (-22.8, 1.5), Intercept b: (-34.1, 68.2); Correlation: r -0.73, r^2 0.54, t -3.26, P (permutation) **<0.0016**). Transects that exhibited the greatest relative *A. bicaorum* declines were positively correlated with highest disturbance.

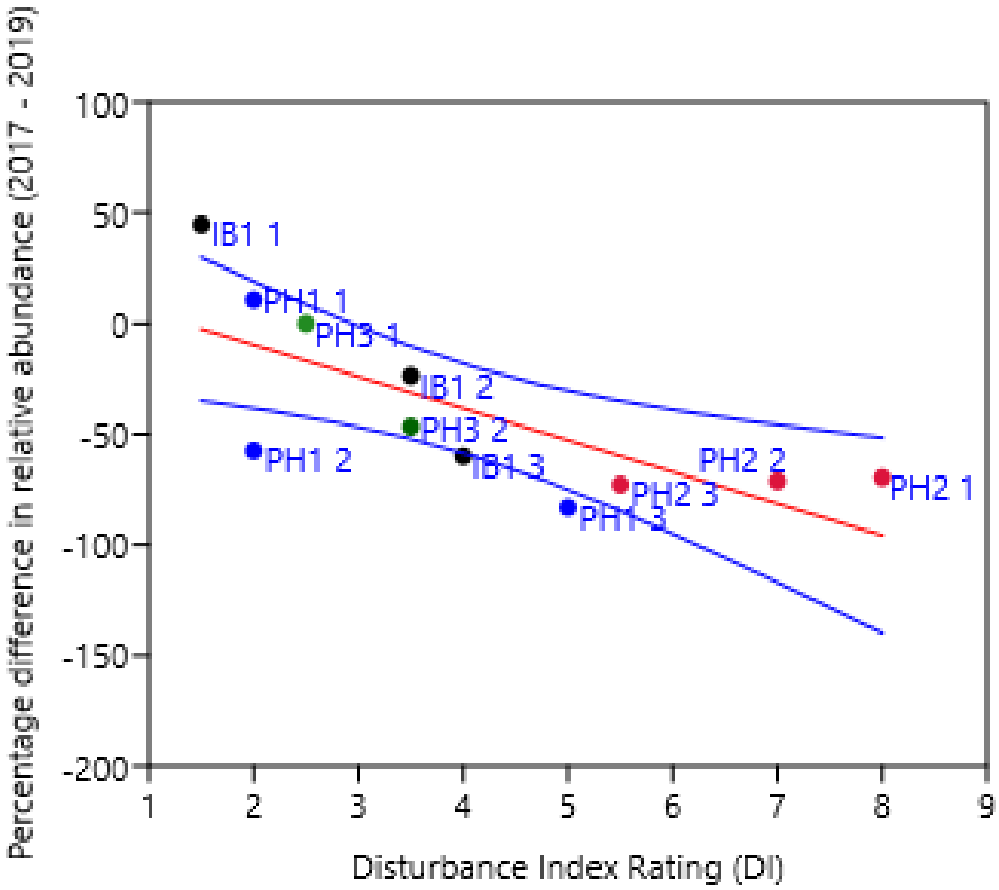


Figure 32. A significant regression of percentage decline in relative abundance against disturbance index scores for the three transects at each site (Table 13). *P-value* <**0.0016**

While the DI categorisation is qualitative and weighted all forms of disturbance equally, my results strongly suggest that high disturbance levels (i.e. the combined and potentially synergistic effects of multiple anthropogenic factors) have contributed to *A. bicaorum* population decline. It is possible that transects which increased in *A. bicaorum* abundance (e.g. IB1 T1) may have done so because of anole migration from neighbouring transects that suffered greater disturbance. On the other hand, those that suffered decline which was not relative to their disturbance level (e.g. PH1 T2), may have been skewed by the edge effects of higher disturbance on a neighbouring transect, or alternatively impacted more heavily by one form of disturbance (e.g. fire). PH3 did not follow the same pattern of decline as other sites, most likely because the site was already post-disturbance in 2017, and its relative disturbance level did not increase radically between sample years. PH3 T3 was exempt from my OLS regression given its infinite (∞) percentage increase from 0-8 individuals. That increase however, I suggest was probably caused by the migration of individuals evading roadside disturbance on the other two transects; given capture rates at PH3 in both years remained equal.

3.2.6: Density estimates

An estimate of the relative population density (number of individuals per unit area) is generally preferred over an estimate of relative abundance, because it allows comparisons among species over space and time. To work through an example of a density index in Table 10, in total 134 anoles were captured in 2017 at site PH1 (an estimated population size of 216.1 using the Schnabel Index). Three transects of 150m compose PH1, and each transect was searched at a fix width of 10m perpendicular each side. This means the total area of site PH1 is 9000m^2 or 0.9 ha (i.e. 3 x 3000m^2 or 0.3 ha transects [150 m × 20 m]). Accordingly, the 2017 density of *A. bicaorum* at site PH1 was between 149 – 240 per ha. On average all sites considered, relative density ranged from 49-240 (µ 150) per hectare in 2017, declining by c. 39% to 41 – 148 (µ 92) per ha by 2019.

Table 10. Density estimates (per ha) and range for each site. Lower limits were calculated using the total area/individuals captured, whereas upper limits were predicted using total area/Schnabel index results. Density estimates that decreased highlighted in bold.

Site	Area (m^2)	Year	Captured	Estimated	Density Range
PH1	9000	2017	134	216	149 – 240
		2019	63	133	**70 – 148**
PH2	9000	2017	113	169	125 -188
		2019	37	48	**41 - 54**
PH3	6000	2017	29	30	49 – 50
		2019	29	35	48 – 58
IB1	6000	2017	56	73	93 – 121
		2019	39	65	**65 – 108**

To give a statistical analysis more power, I calculated density estimates for each transect independently, which identified declines in *A. bicaorum* density at 7/12 transects surveyed in 2019 (Table 11). Considering the transect data from all sites, the predicted 'worse and best case scenario' for *A. bicaorum* density in the sampled forest habitats was between 0 – 393 anoles per ha in 2017 and between 20 – 215 per ha by 2019.

Table 11. Density estimates and range for each transect within the sites. Lower limits were obtained using the individuals captured/ total area, whereas upper limits were predicted using Schnabel index estimates/ total area. Bold highlights represent 2019 transect results that decreased in population density (no overlap with 2017). All density values presented as anoles per hectare.

Site	Transect	Area (m^2)	2017			2019		
			Captured	Estimated	Density Range	Captured	Estimates	Density Range
PH1	T1	3000	24	28	80 - 93	21	31	70 -103
	T2	3000	47	94	157 - 313	22	40	**73 -133**
	T3	3000	63	118	210 - 393	10	20	**33-66**
PH2	T1	3000	17	23	57 - 77	6	7	**20 - 23**
	T2	3000	49	66	163 - 220	14	19	**46 - 63**
	T3	3000	47	81	157 - 270	17	22	**57 - 73**
PH3	T1	2000	19	19	95	15	19	75 - 95
	T2	2000	10	14	50 - 70	7	8	**35 - 40**
	T3	2000	0	0	0	7	8	35 - 40
IB1	T1	2000	26	29	130 - 145	20	43	100 - 215
	T2	2000	25	38	125 - 190	17	29	85 - 145
	T3	2000	5	5	25	2	2	**10**

The mean density estimates of 12 transects in 2017 ranged between 104-158 *A. bicaorum* per hectare, which is nearly double that of the 2019 mean estimate; 53-84. Prior to statistical comparison, the Shapiro-Wilk test confirmed a normal distribution in the annual transect densities calculated from both raw capture data and Schnabel index abundance estimates (N = 12, S-W = 0.971 [2017]; 0.965 [2019], *P* = >0.05). A paired t-test confirmed a significant decline in the raw capture-based density estimate (μ difference = 51, 95% conf. = 14 - 88, t = 3.0301, *P* = <**0.05**), and a marginally significant decline in the relative abundance-based estimate (μ difference = 76.5, 95% conf. = 2 - 155, t = 3.0301, *P* (exact) = <**0.053**). Given the density calculation is constructed with the same population data used to generate the Schnabel Index abundance estimates, it can be safely assumed that these apparent declines in *A. bicaorum* density also correlate with the proposed disturbance index (Table 8; Figure 32); OLS regressions plotted a similarly significant correlation between percentage difference in annual transect density with disturbance value ratings (Slope a: -16.5, Std. error a: 3.6, t: 4.64, Intercept b: 33, Std. error b: 17, *P* (slope) <**0.01**; 95% bootstrapped confidence intervals (N=1999): Slope a: (-24.3, -4.3), Intercept b: (-7.9, 77.9) (r = 0.84, r^2 = 0.705, t = -4.64, *P* (permutation) = **0.0011**) – model not included.

3.2.7: Distance Sampling

Preliminary analysis of combined data for both years projected approved patterns of detectability vs distance (Figure 33); the greatest proportion of *A. bicaorum* were observed on or within 1 m of the transect line, demonstrating a practical asymptotic decrease as distance from the transect line increased. This pattern satisfies the distance sampling assumption that individuals are detected in their original locations, and my observations indicate *A. bicaorum* do not exhibit any evasive movement away from observers on survey. My data possesses a distinctly short-shoulder; this immediately steep decline in observations made at distances greater than 1 m indicates my detection rate was very unlikely to be 100% within a fixed 10m width from the transect, as is assumed by the prior relative abundance indexes (3.2.4). For my distance sampling analysis, I right-truncated data to an appropriate 6m distance (0.15 detection probability – Buckland et al. 2001) to retain the majority of my dataset in the model and discard spurious frequencies of encounters made at a >6m distance which may have otherwise biased estimates. Truncated analysis included 372/ 419 encounters in 2017 and 202/226 in 2019.

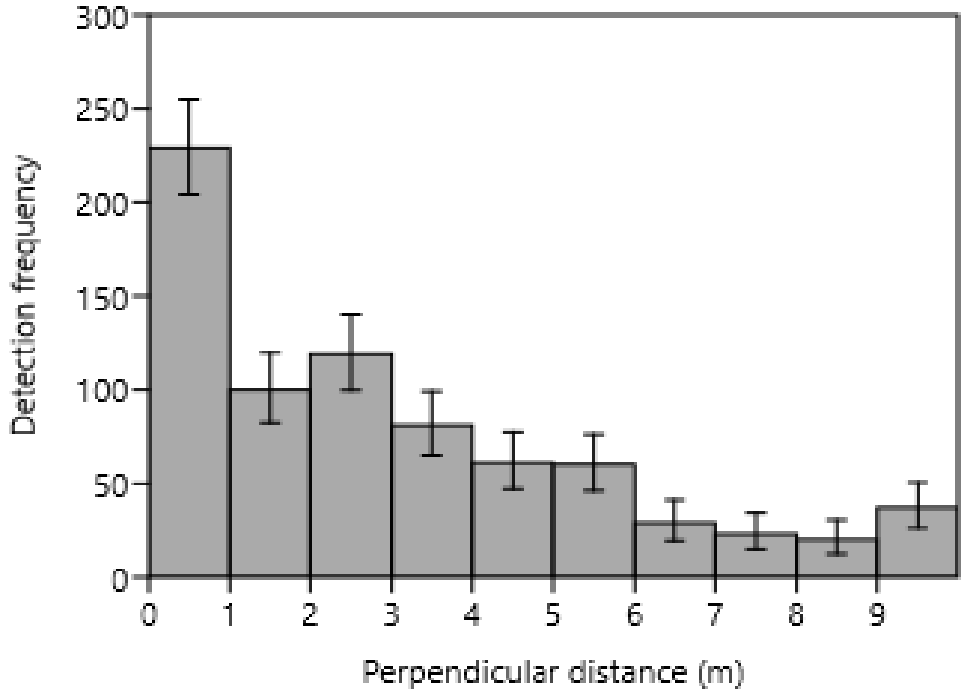


Figure 33. A histogram showing the pooled 2017 & 2019 data for detection distance of encounters. The quantity of detected *A. bicaorum* declined with greater perpendicular distance from the transect line.

Density per hectare and an extrapolated estimate of *A. bicaorum* total abundance in hardwood forest habitat (3.45km^2) were calculated for males and females annually (Table 12). Density estimates for males and females were relatively similar. The difference in the mean of M/F estimates in both years varied by only 14 [2017] and 11 [2019] individuals per hectare, as relatively equal sex ratios were detected. That said, more males were detected in 2017, whereas more females were found in 2019. In 2017, 95% confidence intervals ranged from 81 – 277 (µ 150) individuals per hectare in males, and 72 – 254 (µ 136) in females. In 2019, overall density estimations decreased by >50%, ranging from 30 – 132 (µ 63) males and 36 – 152 (µ 74) females per hectare.

Table 12. The results of DISTANCE 7.3 software estimating density of male & female *A. bicaorum* per hectare (D) and (N) their total individual abundance extrapolated for 3.45km^2 (345 ha) of forest habitat. Key to results as follows; Number of sample occasions (k); Quantity of detected *A. bicaorum* (n); Detection Probability (DP); Encounter Rate (ER); Standard Error (SE); Percentage Coefficient of Variable (%CV); Degrees of freedom (DF); 95% Confidence Interval (95% Conf. Interval - Lower & Upper Limits).

Survey Year	*(k)*	*Sex*	*(n)*	*DP*	*ER*	*Result*	*Estimate*	*SE*	*% CV*	*DF*	*95% Conf. Interval*	
2017	36	M	195	88.1	11.9	D	**150**	48	32.2	399.6	81	277
						N	**51,604**	16,623			27,823	95,709
		F	177	85.1	14.9	D	**136**	45	32.7	386.1	73	254
						N	**46,840**	15,348			25,000	87,762
2019		M	93	87.7	12.3	D	**63**	29	38.6	233.8	30	132
						N	**21,861**	8447			10,483	45,588
		F	109	91.2	8.8	D	**74**	28	37.9	228.4	36	153
						N	**25,622**	9712			12,448	52,740

The 'global density' or pooled estimation was generated by summing the results of sex-specific estimates (Table 13). In 2017 the average *A. bicaorum* density estimate was 285 individuals per hectare (95% conf. = 156 – 521 per ha); decreasing by >50% in 2019 to 138 (95% conf. = 68 – 280 per ha). Detection probability (DP) and encounter rates (ER) of males and females did not vary much between years; detection function was analysed by pooling the distance intervals of both sexes into a single graph of encounters per year (Figure 34 & 35).

Both years' data provided a good fit under the Hazard-rate cosine model. In accordance with Buckland et al. (1993), a model is a good fit if the *p*-value is not significant at the 5% level. The modelled 2017 and 2019 data meets this requirement; a goodness of fit $P = 0.30121$ (2017; $Chi^2 = 3.66$, DF = 3) and $P = 0.14421$ (2019; $Chi^2 = 5.41$, DF = 3) was obtained (Figure 34 & 35). The mean pooled *A. bicaorum* estimations indicate an apparent 51.8% decline in total relative abundance from 98,444 (95% conf. = 53,906 - 179,782) individuals to 47,483 (23,348 – 96,567). Considering my search effort was consistent between sample years, it seems likely that increasing disturbance levels are responsible for the decrease in *A. bicaorum* abundance.

Table 13. The pooled estimation for annual *A. bicaorum* encounters, i.e. density per hectare (D) and (N) their total individual abundance extrapolated for 3.45km^2 (345 ha) of forest habitat. Key to results as follows; Number of sample occasions (k); Akaike's Information Criteria (AIC value); Effective Strip Width in meters (ESW); Quantity of detected *A. bicaorum* (n); Percentage Coefficient of Variable (%CV); Degrees of Freedom (DF); 95% Confidence Intervals (95% Conf. Interval - Lower & Upper Limits).

Survey Year	*(k)*	*AIC*	*ESW*	*(n)*	*Result*	*Estimate*	*%CV*	*DF*	*95% Conf. Interval*	
2017	36	1129.41	1.45	372	D	**285**	31.37	415.97	156	521
					N	**98,444**			53,906	179,782
2019		625.73	1.63	202	D	**138**	37.22	221.73	68	280
					N	**47,483**			23,348	96,567

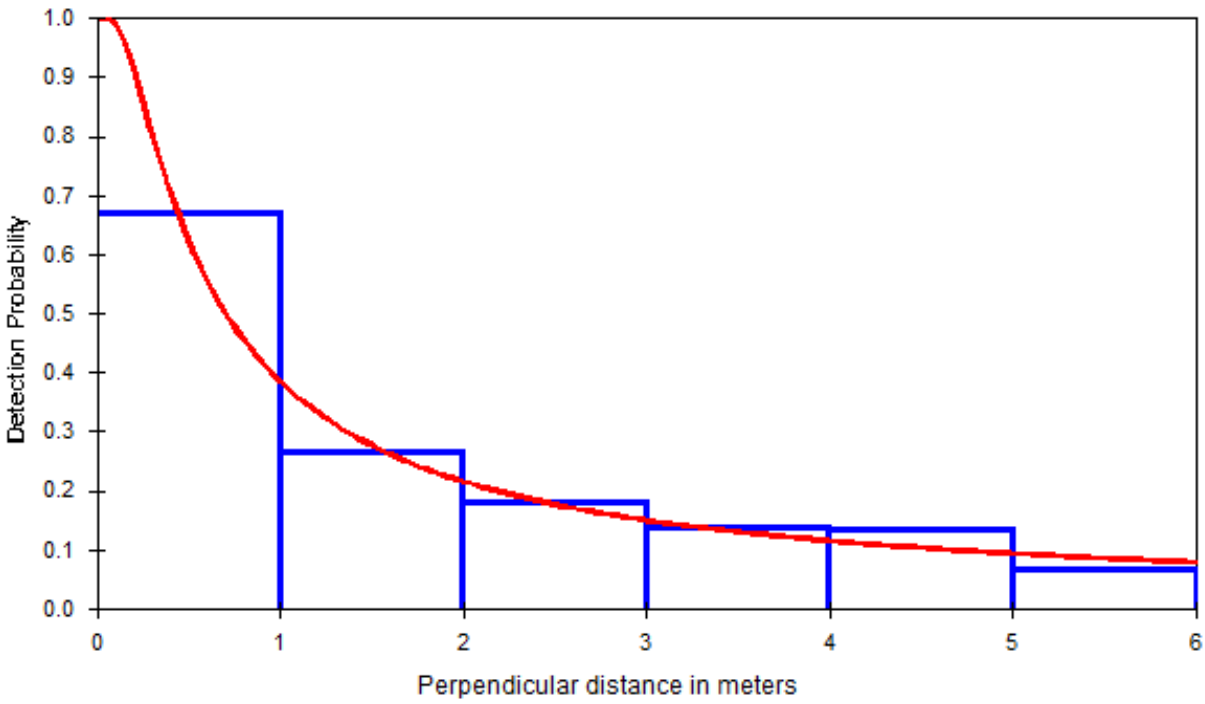


Figure 34. Graph of 2017 Detection Function generated by DISTANCE 7.3. Total Chi-square value = 3.66; Degrees of Freedom = 3; Probability of a greater chi-square value, P = 0.30121

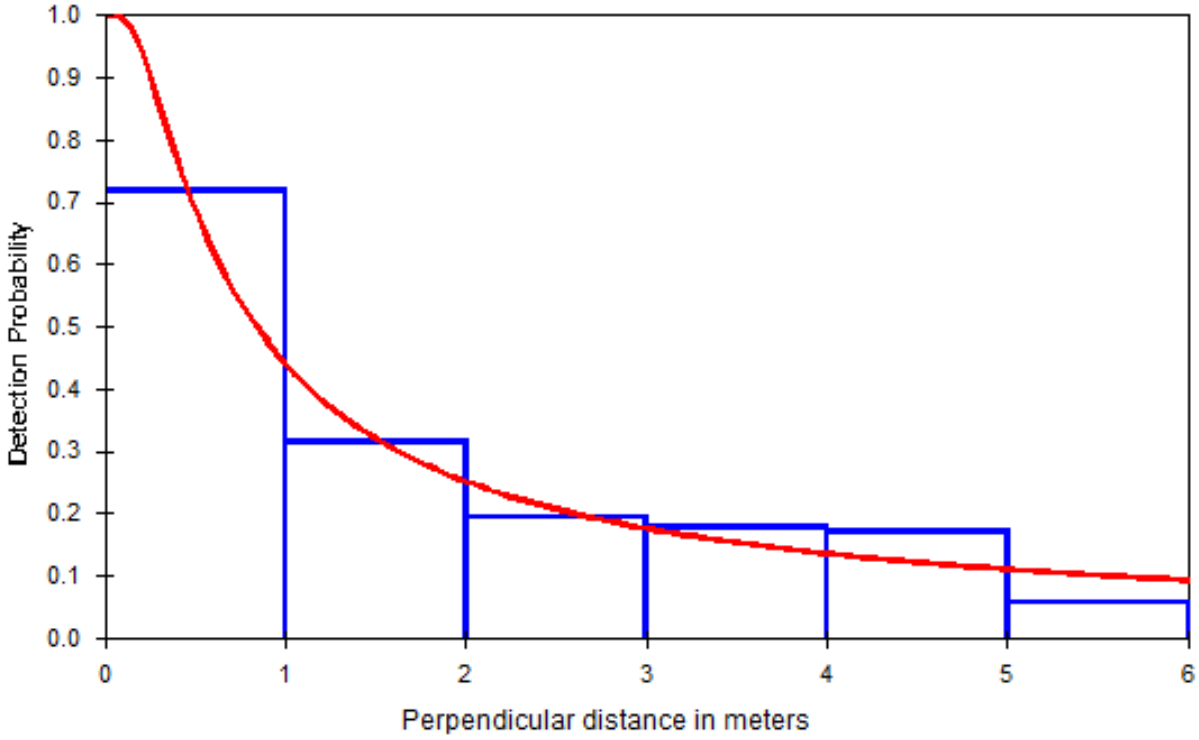


Figure 35. Graph of 2019 Detection Function generated by DISTANCE 7.3. Total Chi-square value = 5.41; Degrees of Freedom = 3; Probability of a greater chi-square value, *P* = 0.14421.

As described by Buckland *et al*. (2001), I used a two tailed *z*-test to compare the results of male-female annual density estimates, which compares two population means with known population standard deviations (SD); Standard error (SE) is equivalent to SD of the theoretical distribution of a population estimate (Table 12). The significance or alpha level (α) was set as 0.05, as the density estimates were generated with 95% confidence. My null hypothesis (corresponding to the assumption of no effect) predicted that no significant difference would be present in the annual density estimates, whereas the alternative hypothesis was that a significant change would be detected between years. The z-test detected a significant difference between the annual density estimates of either sex (Males; Z = 19.05, Z_c = 1.96, P = **<0.0001**; Female: Z =14.34, Z_c = 1.96; P = <**0.0001)**. The z-values were greater than the critical z value (z_c = 1.96) and the resulting p-values were lower than α 0.05; therefore the null hypothesis of equal annual estimates can be safely rejected. The 95% confidence intervals indicate the significant differences between 2017 and 2019 annual density estimates of males are in the region of between 78< − <96 individuals per ha, and 53< − <70 per ha in females.

To verify results, I tested for differences in the absolute density of *A. bicaorum* (the sum of male-female mean estimates with SE & SD calculated from %CV = Table 13) i.e. 2017: N 372, μ 285, SD 89.4; 2019: N 202, μ 138, SD 51.4. A significant difference was detected allowing me to reject the null hypothesis and confirm a significant decline in overall density (Z = 25, Z_c = 1.64; P = <**0.0001**). Overall declines are in the region of 95% conf. 135<− <158 per ha.

3.3: Discussion

3.3.1: Which measure of abundance was best for informing conservation management?

Capture-mark-recapture indices and distance sampling can be used to assess population trends through time, and these trends can be examined to assess the relationships between species and ongoing threats such as disturbance (Lettink & Armstrong, 2003; Amstrup et al. 2006; Buckland et al. 2015). However, important differences exist in the assumptions and analysis of these methods, and while I used both to determine anole counts and trends along transects, it is not correct to assume they will produce comparable results. Though variance in the results and the reliability of these analytical approaches exist, collectively I found them all to be useful from a conservation management perspective. I delineate my key results in the following.

The first portion of my CMR analysis addressed the issue of differences in search effort to later adjust interpretation of relative abundance and density measures. I ascertained using search time, survey speed, and recapture rates (Figure 22; 23; 25; 26), that while my search effort and detection rates were annually consistent, indirect (CPUE – Figure 24) and direct methods of assessing *A. bicaorum* relative abundance and/or density demonstrate a significant decline in population size between sampling years.

Of my index-based analysis, I considered the Schnabel index to be the most reliable method to analyse my CMR data, because fundamentally, the accuracy of weighted estimates increase with the number of sampling occasions and recaptures (Alcoy et al. 2013), and Lincoln Index may be prone to overestimation (Seber, 1973; Amstrup et al. 2006). The latter implies that biologists should use the Schnabel index over the Lincoln index in all available circumstances. However, as indicated by my study results (Figure 27-30), there was no significant difference between those estimates produced by the Lincoln and Schnabel index (Figure 31). This proves consistency in new detections and stable recapture rates during the sampling periods, but infers that the rate of new individuals did not always reach a plateau where recaptures exceeded new capture rates by the final survey (Table 6).

As is proven to be the case in other wildlife (Cattadori et al. 2003), I found CPUE to be an easy and accurate indirect measure of relative abundance and density between sites (Table 5). While CPUE represent changes in detectability that are not necessarily linked directly with changes in abundance, the overall results were comparable to the trends of inter-annual variance and intra-annual decline demonstrated using direct abundance measures (Table 5). As CPUE results implied, the Schnabel index estimates generated for transects demonstrate that relative abundance in 2017 is not entirely uniform between survey sites (Figure 30). The subsequent relative density estimates generated from the Schnabel index, suggest that range in intra-annual abundance more likely reflects the varying suitability of the different forest habitats, as opposed to differences in the size of sampling area (Table 10 & 11).

While population indices are not considered a robust method for assessing true estimates of the population size, provided a constant proportion of the population is sampled, these calculations are still useful for investigating relative changes in abundance (Santini et al. 2018) and have previously been used to estimate the density of threatened lizards (Cosenday & Rocha, 2016).

Index methods, unlike distance sampling however, are not appropriate to extrapolate across much larger areas (e.g. the entire island), because they do not account for variation in the true density of anoles within and among different habitats and location. Variance within the results of each method stem from the fact that distance sampling analysis adjusts the anole counts for discrepancies in detectability at different distances from the transect line (Figure 34 & 35), while the CMR indices assume a 100% uniform detectability within the transects fixed 10 m perpendicular distance – which is very unlikely to be the case (Figure 33). Owing to the different assumptions these calculations are based upon, distance sampling produces an estimate of the actual *A. bicaorum* density (Table 12 & 13), whereas the index methods produce a relative *A. bicaorum* density that represents an unknown fraction of the population, which is assumed to be proportional to true anole abundance on surveys (Table 10 & 11).

CMR indices only estimate the easily captured portion of the population, and the limitations associated with a fixed-width relative abundance index may lead to underestimations given it fails to account for variances in detectability over distance. Probably for this reason, the results of mean relative density estimates per transect (μ 158 [2017] and μ 81 [2019] - Table 10 & 11) were substantially lower than the absolute density estimate produced using the distance sampling method that accounted for differences in detection probability (2017 = μ 285, 2019 = μ 138; Table 13); the relative density estimates of both years were perhaps consistently underestimated by 45% in 2017 and 41% in 2019, so by that logic, index estimates may represent only a c. 60% proportion of the predicted true population size.

Among the literature, distance sampling is considered a simple method under which bias from assumption violation is well understood (Gonzalez et al. 2017). It is less biased than other methods of estimation using CMR population indices, however, in some studies it is also demonstrated to be less precise (Parmenter et al. 2003), and markedly, even underestimate the true densities of some lizards because reptiles may violate typical patterns of distance-detection (Smolensky & Fitzgerald, 2010). I did not consider this to be the case in my study however, given distance sampling produced a higher mean density estimate than index-based methods, and both annual distance models had a satisfactory 'chi^2 goodness of fit' (Figure 34 & 35); detection probability on the transect line was c. 70% during both survey years. Anoles tend to have a more sedentary nature compared to other diurnal lizards, meaning they do not move to evade observers during survey and are unlikely to exhibit great bias in the 100% detection rate assumed within 1m of the transect line.

I considered the distance sampling results to represent a more robust density estimate than those produced from the relative density index, and therefore selected them for the purpose of informing an IUCN conservation assessment (Appendix 2). Distance sampling was a beneficial component of the IUCN assessment, because it enabled me to extrapolate true density to get an absolute count of *A. bicaorum* abundance within the available 3.45km^2 of hardwood forest (Table 13); considered to be the primary habitat of *A. bicaorum*, as indicated by opportunistic occurrence data (Figure 12A). An estimate of total population size is valuable from a conservation management perspective as it gauges the immediate extinction risk of a species; for that reason, I also felt the distance estimates were more appropriate, because stating the lower density estimate that is predisposed to a fixed-width detection-bias could be considered especially misleading and alarmist, especially when a higher estimate is available.

My observations and the literature suggest the 3.45km^2 area of hardwood forest contains the greatest proportion of the islands *A. bicaorum* population, and based on present information it is safe to deduce *A. bicaorum* specialises in this habitat (2.3.1). However, it should be reiterated that as *A. bicaorum* were encountered within alternative habitats and zones of transition (Figure 10), my total abundance estimate generated from multiplying density by the area of hardwood forest, may be more properly defined as an estimation of total abundance within its 'preferred habitat', not true island wide abundance. The presence of *A. bicaorum* in marginal habitats means the absolute abundance in forest is likely to be a slight underestimate of total island population size, and a better stratified sample design within different habitats (such as swamp forest) may have been appropriate to get a more robust absolute estimate and support assumptions based on presence-encounter data.

That said, my field observations and literature suggest the occurrence of *A. bicaorum* in other habitat types is minimal (2.3.1). For my main study design, I considered the potential error in the total population estimate calculated using data from only hardwood forest habitats a worthwhile trade-off to ensure I was able to collect a large *A. bicaorum* morphological dataset and accurate information on the populations in those regions. This was imperative because hardwood forest is disproportionately at greatest risk from anthropogenic activities and it comprises the smallest percentage area of natural habitat on Utila (i.e. only 8.4% of the total island – Table 1). With *A. bicaorum* populations seeming dependent on this naturally-restricted and rapidly diminishing habitat zone, I considered it an utmost conservation priority to determine not only their population size, but also trend within this keystone habitat.

Are *A. bicaorum* populations declining in response to rapid habitat degradation?

Irrespective of the method used to indirectly or directly measure abundance or density, the pattern in my results remained broadly the same. The chief similarity is the inference or detection of a significant c. 40-50% decline in *A. bicaorum* populations from 2017-2019. Mean number of *A. bicaorum* detected on surveys declined by 51.5% (3.2; Table 6), which relative to variation in search effort, equates to a significant 44% decline in CPUE (Table 5; Figure 24). Schnabel index abundance estimates declined by an average 52% (3.2.5), and relative density calculated from those abundance estimates declined by 39% (Table 11). Lastly, extrapolated absolute density using distance sampling detected a significant 51.4% decline in absolute density (3.2.7; Table 13), representing a significant 58% decline in males and 46% decline in females per hectare (Table 12). Notably, the 95% confidence interval generated by the paired t-test showing significant declines in relative density (95% conf. 2-155 per ha), did at its upper-most limits overlap with that of the *z*-test on absolute density estimate (95% conf. 135<− <158).

Given comparable trends of decline were detected throughout my analysis, I deduce that index calculations of relative abundance are proportional to the distance-sampling predicted trends in true anole abundance. The uniformity of these results probably relates to the fact that input data are intrinsically linked, however, identifying a significant relative trend of decline using separate analysis grounded on different assumptions, upholds the robustness of my dataset and the integrity of concluding results.

Though it is tempting to conclude from the overall population data that *A. bicaorum* has declined rapidly at sites in response to habitat degradation (primarily owing to understory clearance, tree felling and fire (3.1.1; Table 8; Figure 32), I am cautious not to attribute direct causation for this decline. My study is limited by its relatively small sample size (both in its two-year duration and four survey sites) and more so by an absence of quantitative site habitat data prior to modification. As habitat changes were subjectively quantified at each site, it is important that my overall results on disturbance-driven trends are interpreted with some restraint. The significant correlation I detected between disturbance index ratings and percentage change in relative abundance (Figure 32) and density (3.2.6), may not solely be attributed to changes in actual abundance, but due to changes detectability across space and years, especially as this includes ongoing disturbance events.

Continued monitoring of abundance trends are still needed to confirm whether the results reflect natural fluctuations in *A. bicaorum* populations or an ongoing decline in response to disturbance. All limitations considered however, the assumption that my preliminary results represent a catastrophic population decline in *A. bicaorum* is not farfetched, as the impacts associated with deforestation and habitat loss are considered the single largest factor contributing to herpetofauna decline (Todd et al. 2010). The effects of such are amplified and especially damaging to specialist island species where habitat and resources are naturally limited and migration is restricted to the available land mass (Wilson & Peter 1988; Tershy et al. 2015; Spatz et al. 2017).

4: Population morphology

4.1 Data analysis

Data for my analysis was collected during VES surveys as described in methods section 3.1.3. I focused my analysis on comparing male-female morphology by site, as I did not expect any differences to be detected among transects at each site. Although it was appropriate to treat each transect as a closed-population during the short course of 3-day population estimates, to look at trends in adaptive morphology across longer phases through time, I considered that populations on each transect within sites were interconnected and collectively influenced by the same ecological variables due to the close proximity and parallel environmental conditions.

I first used a basic statistical summary to describe the range of annual morphological data collected for males and females on a whole (SVL, body mass, dewlap and tail length); to later compare to min-max sizes of morphology stated in current literature. Using my field notes, I calculated and compared the annual percentage frequency of tail-breakage in the population, the size-based age ratio (adult, sub-adult, juvenile) and sex ratio of my sample set (the number of male anoles per 100 females).

Sexual dimorphism

For morphological comparisons between sexes, Mann-Whitney U tests were used to test for differences in male-female morphology (SVL, body mass, tail and dewlap length). However, because this method of analysis did not remove the effect of body size on morphological traits, an ANCOVA was used (with SVL as a covariate) to confirm which morphological aspects were sexually dimorphic relative to SVL.

Morphological variance between sites and combined site changes between years

To examine whether morphological variation was present among *A. bicaorum* populations, ANOVA were used to determine whether mean SVL varied significantly. Dunn's post-hoc tests (Bonferroni *p*-value) were included alongside significant ANOVA results, to demonstrate which site comparisons had tested significantly different. ANCOVA (using SVL as a covariate) were used to determine variation in body mass and dewlap length among the sample sites each year. A series of two-sample t-tests were then used to determine any significant annual differences in site morphology between years. A separate ANCOVA was then performed using the combined data of all sites to compare morphological changes between years.

Body Condition Index

I calculated a Body Condition Score/Index (BCI) for males and females by dividing body mass by SVL to provide a ratio. Independent t-tests were used determine if significant differences were present in the body condition of males and females either year, and then used to compare whether body condition had changed within males and females between years. To examine whether body condition interacted significantly with the dewlap size of either sex, I regressed relative dewlap size (dewlap length/SVL against body condition) and performed an ANCOVA

Annual changes and trends in morphology between sites

To determine whether SVL had changed significantly between years at any given site, independent t-tests were conducted by sex, site and year. ANCOVA using SVL as a covariate, were then applied to test for site changes in male-female dewlap length and body mass. To minimise type 1 errors associated with running numerous statistical comparisons between four survey sites (i.e. more than two sample sets), I applied a Bonferroni correction to the original α value of those results ($P = 0.05/4$) to test for critical significance at α level 0.0125.

Sexual Size Dimorphism (SSD) and Relative Density

To determine whether the morphology of males and females correlated with population density, a value representing sexual size dimorphism (SSD) was calculated for SVL, relative body mass and dewlap size at each site. Sexual size dimorphism (SSD) was calculated by dividing the mean of male-female morphological values to obtain the difference. The effect of body size on dewlap length and body mass was removed by dividing those values for each sex by SVL, before taking a mean for each site and dividing male-female values to compute relative dimorphism in those traits. Those SSD ratios were then compared to mean relative density estimate for each site using an Ordinary Least Squares (OLS) Regression model.

4.2: Results

Throughout the duration of the study at all four sample sites, I collected morphometric data on 395 (304 adult; 76 sub-adult; 15 juvenile) individuals that consisted of 192 confirmed males and 195 females (Displayed by year –Table 14). The sex ratio (Table 14 - [SR]) was calculated as the number of male anoles per 100 females. As a whole, the ratio of males to females was well balanced but did fluctuate between sample years i.e. 109 males per every 100 females in 2017, as appose to 80 per 100 in 2019; an approximate 1.1:1 M:F ratio in 2017 vs 1: 1.3 in 2019. The number of mature males did decline in 2019 (Table 15), and the effect of this was reflected in the prior DISTANCE density estimations calculated for each sex (Table 12).

To provide general morphological descriptions for *A. bicaorum*, I initially combined the data from all sites to obtain averages for SVL, weight and dewlap length by sample year. The mean SVL of individuals across all sites in 2017 was 63mm (45-76mm) in males and 61mm (43-70mm) in females. In 2019, I report similar averages of 66mm (45-75mm) in males and 62mm (41-72) in females. In part to them being longer in SVL, males were also on average heavier than females (2017 = 6.7g [2-9.4g] in males and 6.1g [2-8.8g] in females; 2019 = 5.78g [2-8.5g] in males and 5.77g [2-9g] in females). Dewlap size (mm) was also greater in males (2017 = 33.3mm [11 – 44mm] in males vs 11.7 mm [4 – 21mm in females]; 2019 = 31.2 [15-41mm] in males vs 13.7 [9-18mm] in females).

Descriptions for tail length were obtained in a separate analysis excluding those individuals with signs of prior caudal autonomy, alongside determining the percentage frequency of tail loss in populations. Males were found to have a greater tail length than females, probably also in part to their greater body size; (2017 = 135.5mm [105 - 161mm] in males and 128.4mm [106-157mm] in females; 2019 = 130.9mm [91-156mm] in males and 128.4 [92-151mm] in females). Notably, the overall accuracy of this tail length data should be interpreted with scrutiny, as bias towards shorter average lengths could arise owing to the difficulties of accurately determining full ‘intact’ tails, from ones that had partially regrown or just lost a small portion of their tip. Nonetheless, tail break frequency occurred at relatively equal rates in both males and females between sample years (Table 15). Overall, tail loss and/or regrowth was present in approximately 25-30% of the sampled population. Caudal autotomy or tail loss may reflect predation rates and efficiency (Bateman & Fleming, 2011) or intraspecific competition rates (Itescu et al. 2017).

Table 14. Descriptive statistics for various measurements of morphology, given as the mean value followed by min-max (∧-∨) range. Key to abbreviations as follows; Total Measured (TM); Age ratio (AR = Adult = >60mm; Sub-Adult = 50–60mm; Juvenile = <50mm); Total Sexed (TS); Sex Ratio – number of males per 100 females (SR = [m/f] x 100); Snout-Vent-Length (SVL - mm); Tail Length (TL - mm); Weight (WT – g); Dewlap Size (D - mm).

Year	*TM*	*AR*	*Sex*	*TS*	*SR*	*SVL*	∧-∨	*WT*	∧-∨	*D*	∧-∨
2017	259	211; 41; 7	M	133	109.9	63	45-76	6.7	2-9.4	33.3	11-44
			F	121		61.3	43-70	6.1	2-8.8	11.7	4-21
2019	136	93; 35; 8	M	59	79.7	65.5	45-75	5.78	2-8.5	31.2	15-41
			F	74		62	41- 72	5.77	2-9	13.7	9-18

Table 15. Presenting tail data collected for male and female *A. bicaorum* by year. Key to abbreviations as follows; Total Measured (TM); Total individuals with Full Tail (TFT); mean Tail Length (TL – mm); Total individuals with tail break (TTB); Percentage tail break in population (%TB).

Year	*Sex*	*TM*	*TFT*	*TL*	*Min-Max*	*TTB*	*%TB*
2017	M	133	97	135.5	105-161	35	26.31
	F	121	84	128.4	106-157	36	29.75
2019	M	59	43	130.9	91-156	16	27.11
	F	74	53	128.4	92- 151	21	28.37

4.2.1: Sexual dimorphism

SVL data combined by sex from both years had a non-normal distribution (Male: N 176, S-W 0.949; female: N 178, S-W 0.965, *P* = <0.05). A Mann-Whitney U test was used to compare the morphology between sexes. The median value for male SVL was significantly greater than females (Male: µ rank 102.9: Female: µ rank 74.6, M-W 10491, *z* = 5.375, *P* (Monte Carlo) = 0.0001). Percentile graphs demonstrate that sampled males had on average a greater SVL than females in both years (Figure 36), however, the size distinction between sexes was less clear in 2019 data. Other morphological variables (except female tail length) had non-normal distribution (weight: male N 176, S-W 0.974, female N 178, S-W 0.981, *P* = **<0.05**; tail: male N 139, S-W 0.971, *P* = **<0.05**, female N 137, S-W 0.992, *P* = >0.05; dewlap: male N 176, S-W 0.924, *P* = **<0.05**, female N 178, S-W 0.982, *P* = **<0.05**). Likely because of their larger SVL, Mann-Whitney U tests indicated that males had significantly greater weight (Male: µ rank 96.2: Female: µ rank 81.3, M-W 12847, *z* = 2.93, *P* = **0.0025**), tail length (Male: µ rank 79.9: Female: µ rank 58.5, M-W 6708, *z* = 4.24, *P* = **0.0002**), and dewlap length (Male: µ rank 131.9: Female: µ rank 45.6, M-W 203.5, *z* = 16.03, *P* = **0.0001**). However, in order to confirm male-bias sexual dimorphism in the above traits and whether differences in body mass, tail and dewlap length were significantly different relative to SVL, a one-way ANCOVA (using SVL as a covariate) was used to test each morphological variable and remove the effects of body size.

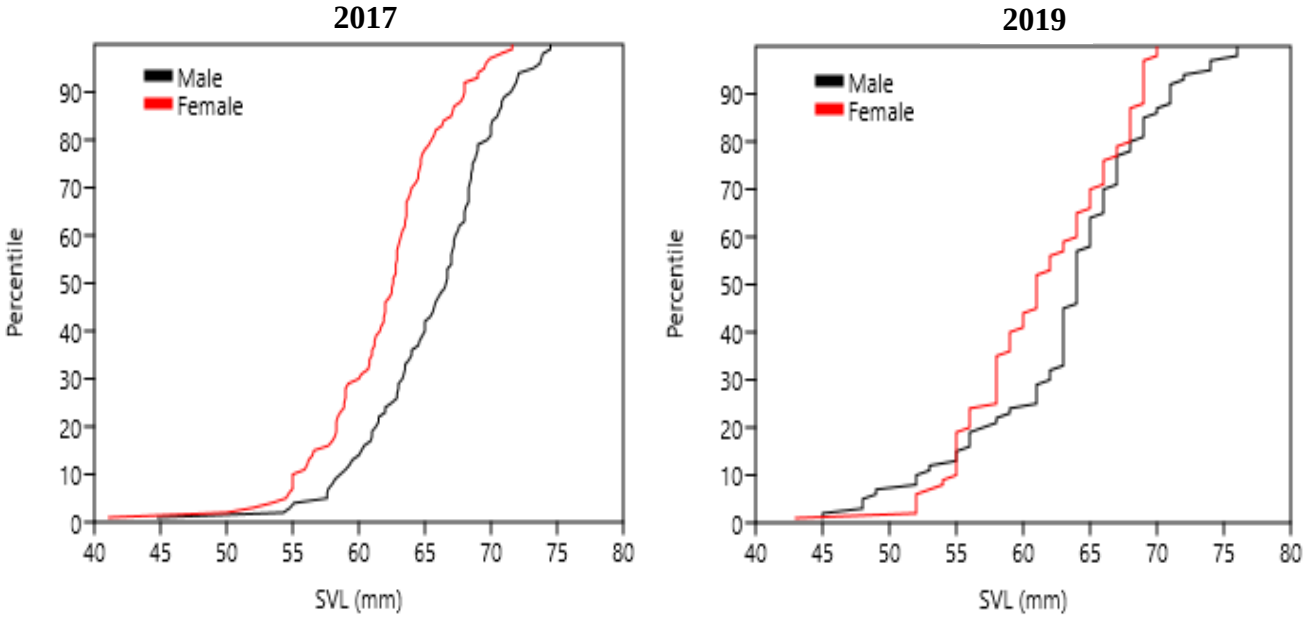


Figure 36. The annual percentile range of male-female SVL (mm). In both years, sampled males had greater SVL than females. However, in 2019, the breadth of sexually dimorphic distinction in body size had reduced, in part to there being less large males in the population.

4.2.2: Body mass relative to SVL

Figure 37 displays the regression of a one-way ANCOVA (SVL as a covariate), that identified a significant difference in the mean weight of males (N 176) and females (N 178, F= 6.168, *P* = 0.01347). In contrast to initial Mann-Whitney U tests, the adjusted mean for weight found females had a significantly greater body mass than males of similar SVL (male μ =6.1, ±0.13; female μ=6.3, ±0.13; F = 6, *P* = **<0.05**). However, there was no significant difference in the homogeneity of slopes (F= 0.2682, *P* = >0.5). The results demonstrate that while males and females grew in SVL and body mass at similar rates, the mean of female weight was significantly heavier than males of the same SVL. While males did reach a greater maximum SVL and weight, the latter were a function of each other. Overall, females were in fact heavier than males in grams per SVL mm, probably due to selective pressures of fecundity and ovulation. Linear models regressing SVL and weight in males and females found significant positive correlations (male: *P* (slope) = **<0.001;** female: *P* (slope) = **<0.001**). Mean adjusted body mass in both sexes was normally distributed (Male, N 117, S-W 0.979; Female, N 104, S-W 0.983, *P* = >0.05**)**, though SVL was not (Male, S-W 0.951; Female, S-W 0.956, *P* = <**0.05).** However, the SVL data do not show substantial skew and ANOVA (and thus ANCOVA) are robust to slight departures from normality (Quinn & Keough, 2020).

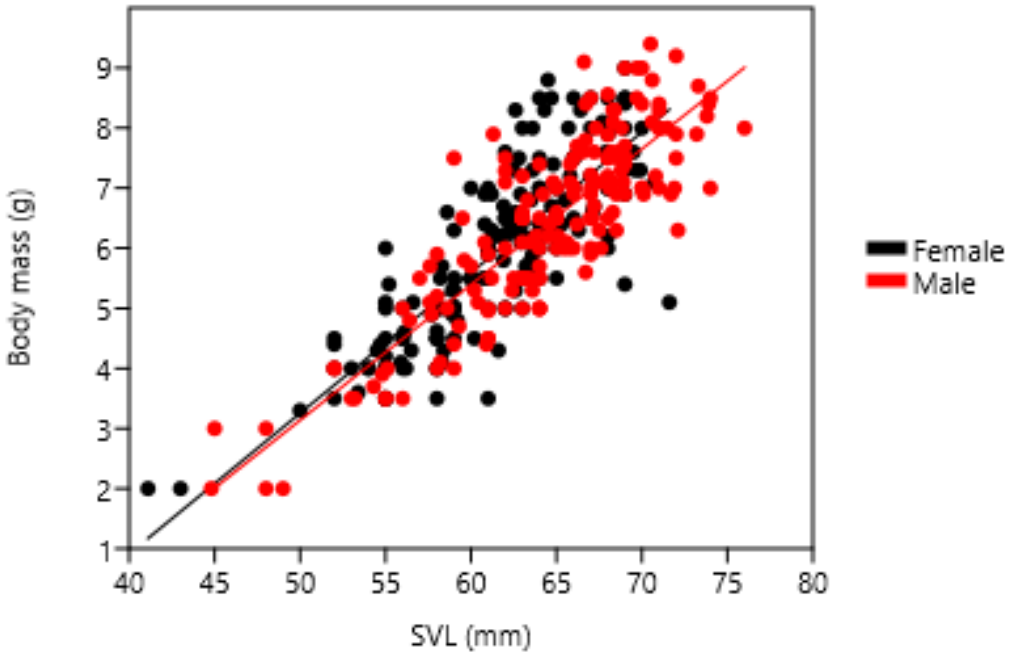


Figure 37. The regressions of male and female body mass by SVL. A one-way ANCOVA for equal means (adjusted using SVL as a covariate) confirmed significantly greater body mass in females (F 6.168, *P* = **0.01347**). Comparison of regressions (homogeneity of slope) detected no significant difference between sexes (F 50.01; *P* (same slope) = 0.6085).

4.2.3: Tail length relative to SVL

After removing the effect of body size, the results of a one-way ANCOVA identified no significant difference in the mean tail length of males and females (F = 0.8531, *P* = 0.3567 – Figure 38). Female (N 113, S-W 0.975) and male SVL (N 114, S-W 0.973) were not normally distributed (*P* = **<0.05**), but relative tail lengths were (female: S-W 0.982; male: S-W 0.984, *P* = >0.05). Using SVL as a covariate, the adjusted mean for male tail length (mm) was only slightly longer than that of similarly sized females (male μ = 131.7 (±1.14); female μ = 130.8 (±1.21), and there was no significant difference (*F* = 0.85; *P* = >0.05). Comparing the regressions of tail length in males and females also found no significant difference in the homogeneity of slope (F = 0.0371, *P* = 0.8474), indicating that tail length grew at the same rate and did not scale differently between the sexes. No substantial skew in SVL was detected, and small violations of normality should have little practical effect on ANCOVA analysis. As both male and female *A. bicaorum* possess near equal tail lengths that are on average over twice their relative SVL, the data affirms basic ecological observations that both sexes are adapted for an arboreal lifestyle. In lizards, long tails imply increased activity in the perch matrix and improved balance in arboreal habitats (Ballinger 1973).

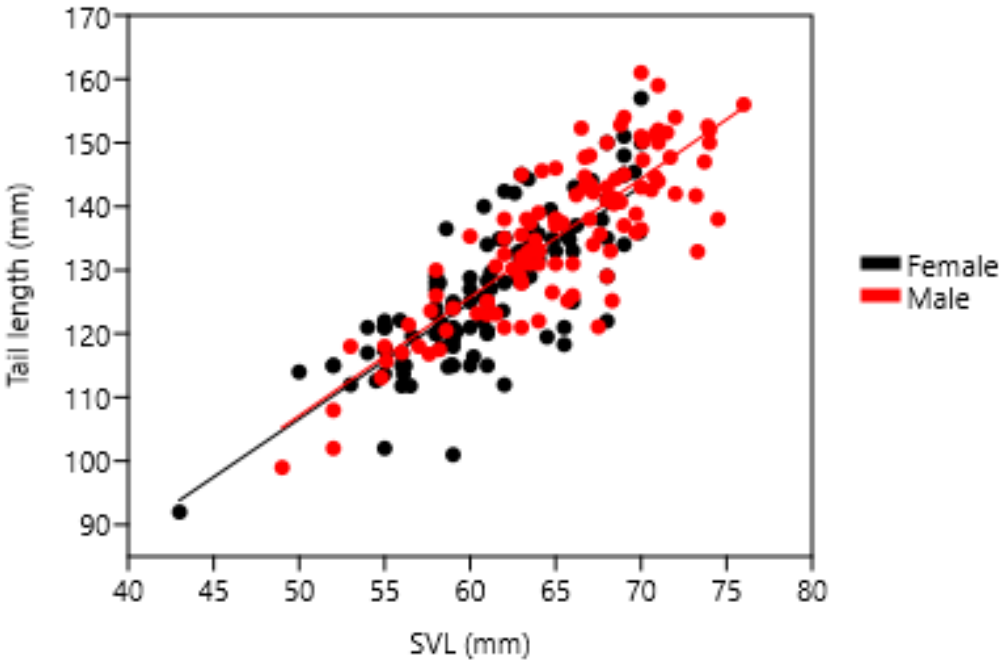


Figure 38. Regression of male and female tail length by SVL. A one-way ANCOVA for equal means (adjusted using SVL as a covariate) confirmed there was no significant difference in tail length between sexes (*F* = 0.85; *P* = >0.05). Homogeneity of slope was also uniform (F = 0.0371, *P* = 0.8474)

4.2.4: Dewlap length relative to SVL

As is expected in anoles, the most evident sexually dimorphic difference was in the dewlap. The results indicated that male *A. bicaorum* dewlaps were on average between 2.2 – 2.8 times larger than those of females were. In males, min-max dewlap length (all ages) ranged from 11-44mm, whereas in females it measured from 4-21mm. I removed outliers in the data prior to 50mm SVL; the sex as determined by dewlap length was not well defined prior to sexual maturity. Dewlap data was normally distributed (male N 165, S-W 0.988, P = 0.17; female N 174, S-W 0.99, P = 0.31), SVL was not (P = <**0.05**). Figure 39 plots a one-way ANCOVA for equal means tested for differences in male-female dewlap length, using SVL as a covariate. This identified significant differences in the mean dewlap length of males and females relative to SVL (DF = 1, F = 3605; P = <**0.001**) with no substantial skew. A significant difference was detected in the homogeneity of slopes (F= 39, P = **<0.001).** The significant interactions between sex and SVL for dewlap length confirm that this sexually dimorphic aspect scaled differently with body length. OLS regressions of dewlap length vs SVL show a positive significant correlation of increasing dewlap size with relative body size in both sexes (male; r^2 = 0.36, t = 9.6**;** female; r^2 = 0.08, t = 3.9, P = **0.0001**). The correlation of increasing dewlap length with SVL is significantly stronger in males than in females. This is unsurprising, considering its role in male courtship and territoriality (Tokarz, R. 2002; Vanhooydonck et al. 2009). The larger dewlap of males implies a greater functional significance relative to females and likely enables signalling across greater territorial distances (Jenssen et al. 2000).

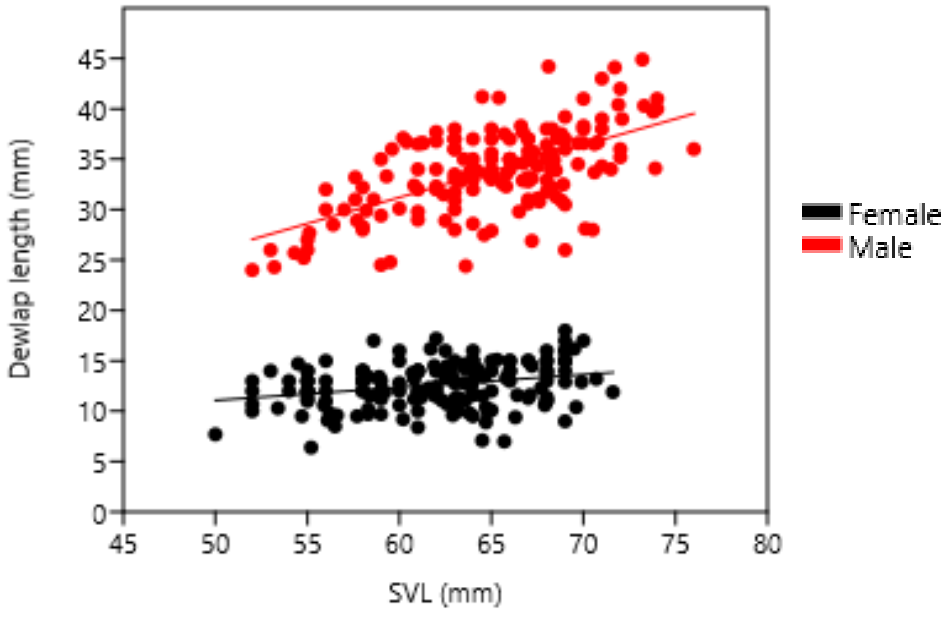


Figure 39. Regression of male and female dewlap length by SVL. A one-way ANCOVA for equal means (adjusted using SVL as a covariate) confirmed a significant difference in the mean length between sexes (F = 3605; P = <**0.001**).

4.2.5: Morphological variation between sample sites each year

In order to investigate morphological variance among sampled *A. bicaorum* populations, morphological features were analysed per site and by year. Given substantial amounts of disturbance and apparent population decline took place at our sites from 2018-19, attention was first focused on analysis of the 2017 site data that best represents the natural dynamics of *A. bicaorum* populations within forest habitat prior to disturbance. The data from 2019 were then analysed separately to identify whether any morphological response had occurred in populations amidst the rising degradation of these forest habitats. A summary of raw data displays annual differences in the morphology of males and females at each site (Table 16).

Table 16. Statistical summary male-female morphological data collected per site annually (excluding tail length).

2017

Site	*Sex*	N	SVL	25-75 percentile	Body mass	25-75 percentile	Dewlap length	25-75 percentile
IB1	M	27	65.3	61.2-68.6	6.5	5.5-7.4	32.7	30.6-36.6
	F	23	62.9	61.6-64.5	6.1	5.4-6.6	11.4	9.8-13.3
PH1	M	22	68.4	66.4-70.7	7.5	6.9-8.4	36.6	34-40.5
	F	25	61.9	58.6-65.6	6.2	4.5-7.5	11.6	9.4-13.4
PH2	M	50	64.8	62.8-68.7	6.8	5.7-7.7	32.6	29.7-35.4
	F	36	60.5	58.1-63.6	5.9	4.7-6.9	11.1	9.9-12.3
PH3	M	16	63.8	59.9-67.5	6.1	5.9-6.6	32.5	30.8-35.4
	F	12	61.4	59.1-63.4	6.2	5.5-6.7	14.4	13.6-15

2019

Site	*Sex*	N	SVL	25-75 percentile	Body mass	25-75 percentile	Dewlap length	25-75 percentile
IB1	M	13	61.4	57-66.5	5.3	4-6.8	31.8	27.5-37
	F	18	59.3	55.8-61.5	4.9	4-5.5	12.9	12-13.3
PH1	M	22	63.7	58.8-68.3	5.9	4.4-7.1	33.6	31.5-38
	F	27	63	59-69	6.4	5-7.5	14.9	13-15
PH2	M	14	62.6	56.8-67.5	5.8	5-.7.5	31.2	29.5-36
	F	17	59.6	55-64	5.5	4.3-6.5	13.5	12.5-15
PH3	M	8	63.3	62.3-66.8	5.7	5-6.5	32.8	27.3-37
	F	13	63.1	59-67.5	6.3	5.2-7.5	14.3	13-15

ANOVA were used to determine whether mean SVL varied significantly between sample sites either year. In 2017, statistical significance was detected in the means of male SVL (F = 4.36, DF = 3, P = **0.0061** – Table 17). No significant difference was present in the means of female SVL among sites (F = 1.265, DF = 3, P = 0.2912). Given the significant ANOVA result, a Dunn post hoc test was included for male SVL to confirm which sites were statistically different. That analysis identified a statistical significance in male SVL between PH1 and most other sites (PH1 vs IB1 = ***0.0221***; PH1 vs PH2 = **0.0036**; PH1 vs PH3 = **0.0023**); males at site PH1 had on average the greatest SVL (Table 18). In 2019, an ANOVA of sites found no statistically significant differences in the SVL of males (F = 0.3174, DF = *3*, P = 0.8127) or females (F = 2.644, DF = 3, P = 0.0557). Apparently, the males at site PH1 in 2019 were no longer significantly larger compared to those of other sites, perhaps indicating a disturbance-driven change in the factor driving prior increased size in 2017.

Table 17. 2017 Male SVL data sorted into four groups based on sample site. ANOVA (equal means) found significant differences.

Male SVL	*N*	*Mean SVL*	*SVL ∧∨*	*St.Dev*	*F value*	*DF*	*P =*
IB1	27	65.3	54.3-73.9	4.8	4.36	3	**0.0061**
PH1	22	68.4	60.4-73.8	3.4			
PH2	50	64.8	54.8-72	4.7			
PH3	16	63.8	53.2-68.5	4.4			

Table 18. *P* value results of Dunns post hoc test analysing data of male SVL (mm) by sample site. Raw *p*-values corrected for sequential Bonferroni significance; PH1 vs IB1 was only significant prior to Bonferroni correction (italic). As is shown, SVL was significantly larger in males at site PH1 when compared to those of males at other sites in 2017.

Male SVL	**IB1**	**PH1**	**PH2**	**PH3**
IB1		***0.0222***	0.7141	0.2777
PH1	***0.0222***		**0.0036**	**0.0024**
PH2	0.7141	**0.0036**		0.3747
PH3	0.2777	**0.0023**	0.3747	

I then used t-tests to evaluate changes in SVL between years, and ANCOVA to compare variance in other morphological traits among sites and years. Combing site data (Table 19), a t-test identified an overall significant decrease in the mean SVL of males (*P* = **0.0118**), but found no significant difference in female SVL between years (*P* = 0.4611).

Table 19. The results of a two-sample t-test for equal means comparing the annual SVL of male and female *A. bicaorum*. *P*-value reported as per the Monte Carlo permutation.

Sex	*Date*	*N*	*Mean*	*Mean difference*	*95% conf.*	*t-test*	*P =*
Male	2017	117	65.3	-2.3	(0.5-4.1)	1.9737	**0.0118**
	2019	59	63				
Female	2017	104	61.9	-0.6	(0.9-2.1)	1.9735	0.4611
	2019	74	61.3				

Comparing morphological traits with the effect of body size removed, no significant differences were present in the means of weight and male dewlap length per site using an ANCOVA that adjusted means using SVL as a covariate (Figure 40; 41 A & B). Therefore, the scale of male features only varied between sites in accordance with their body size. This may relate to the differences in conditions available to them in different forest habitats; suggesting PH1 favours larger males. Interestingly however, those tests did confirm significant differences in PH3 female dewlap size relative to SVL in 2017 (F = 6.376, *P* = **0.00057 -** Figure 40 C), whereas all other morphological site comparisons were non-significant (*P* = >0.05). The same ANCOVA tests were conducted on the 2019 site data, which confirmed that all sites had equal variance in morphology (*P* = >0.05 – Figure 40 D). The significant difference detected in 2017 female dewlap length at PH3 were no longer present in 2019, indicating that a shift in the homogeneity of dewlap length across sites had occurred. As variance in body mass and dewlap length (except PH3 2017 females) was relatively equal between sites independent of SVL (Figure 40 & 41), the results of all sites were combined by year and compared to determine whether any significant annual shifts had occurred in population morphology (Figure 42). Those ANCOVA tests only detected significant annual differences in the mean body mass of males (F = 13.2, *P* = <**0.001**), and the dewlap length of females (F = 44.2, *P* = <**0.001**). Males declined in weight, and female dewlap length increased independent of SVL. Near significant reductions were found in female weight (F = 2.771, *P* = 0.0978). All other morphological aspects were non-significant with the effect of body size removed (*P* = >0.05).

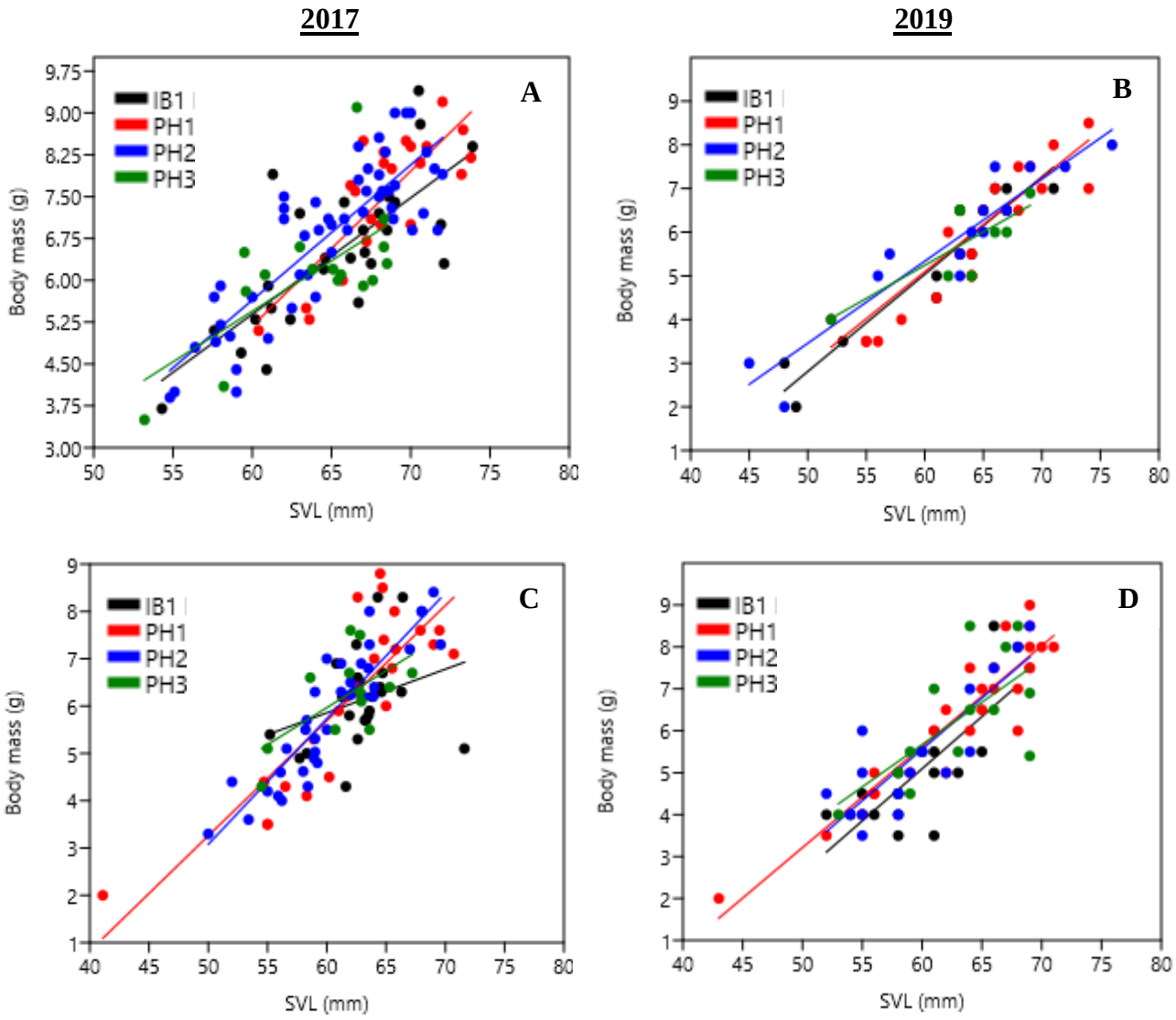


Figure 40. Comparing the values of male and female body mass by SVL, colour coded by site. A one-way ANCOVA for equal means using SVL as a covariate, found no significant difference in the weight of males between 2017 [A] sites (F 2.362, *P* = 0.0752) or 2019 [B] sample sites (F: 0.2928; *P* =: 0.8304**).** The same tests also found no significant difference in the weight of females between 2017 [C] sites (F 7.966, *P* = 0.4989) and 2019 [D] sites (F: 1.66; *P* =: 0.1863).

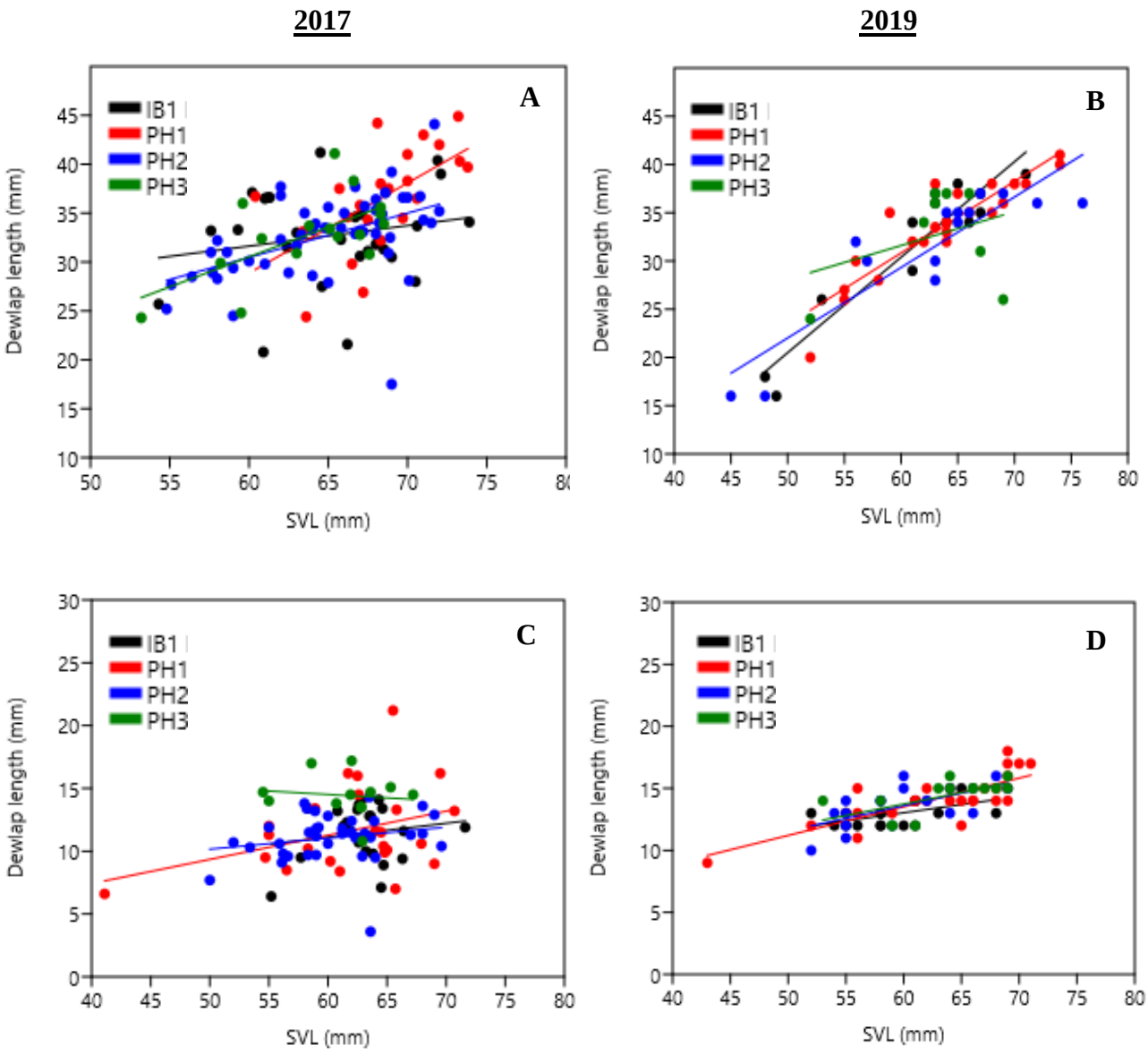


Figure 41. Scatterplot comparing the values of male-female dewlap length and SVL, colour coded by site. A one-way ANCOVA for equal means using SVL as a covariate, found no significant difference in the dewlap length of males between sites in 2017 [A] (F = 1.671, *P* = 0.1774), or in 2019 [B] (F =7.155, *P* =: 0.5495**).** The same tests found a significant difference in the dewlap length of females between sites in 2017 [C] (F = 6.376, *P* = **0.00057**). However, there was no significant difference in 2019 [D] (F = 0.9318, *P* =: 0.4301). PH3 was greater than other sites in 2017 [C], but by 2019 [D], all other sites became homogenous with PH3.

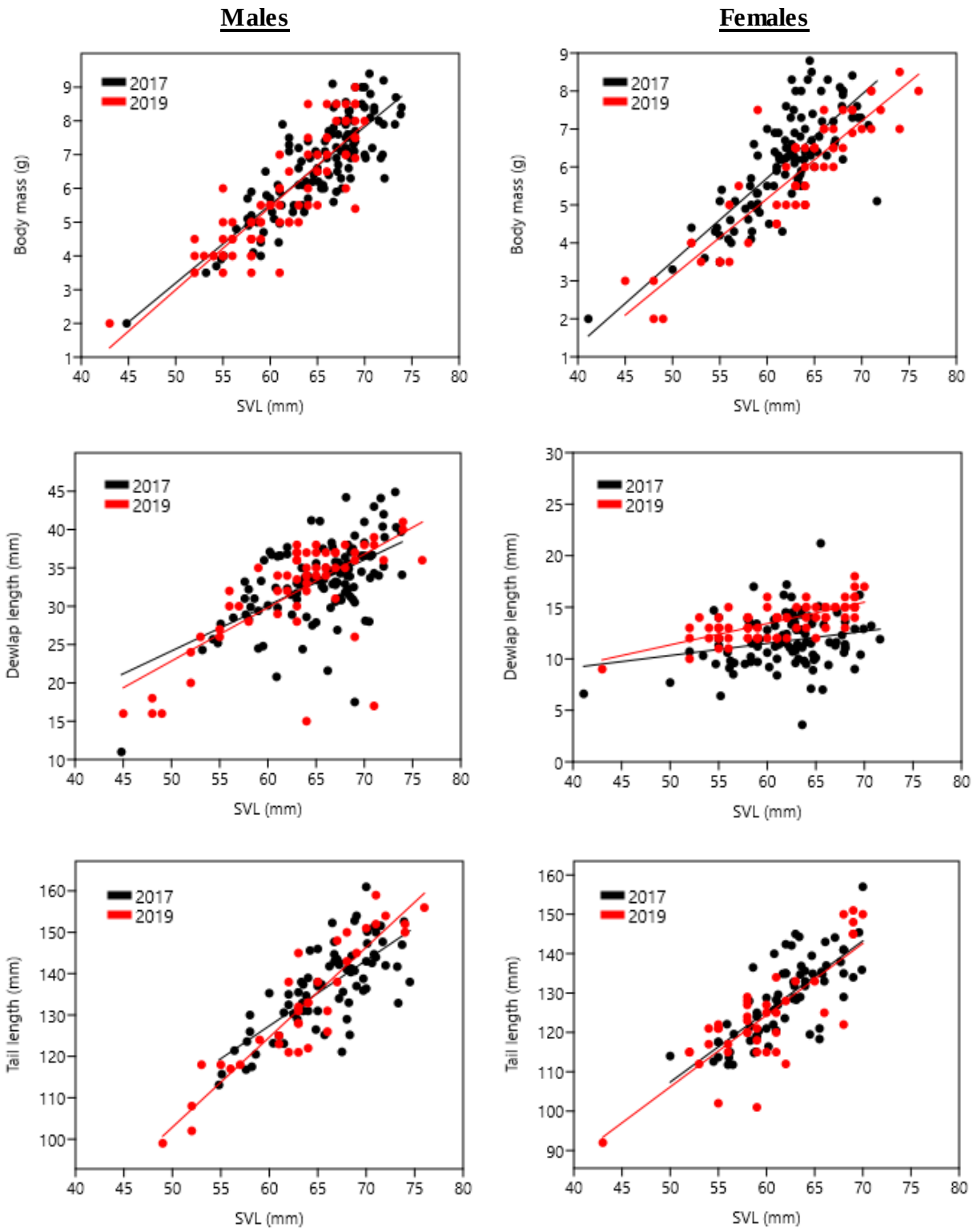


Figure 42. Male and female morphology separated by year. ANCOVA tests for equal means (using SVL as a covariate) only detected significant annual differences in the mean body mass of males (F =13.2, *P*= < **0.001**), and the dewlap length of females (F = 44.2, *P* = <**0.001**). Males declined in weight, and female dewlap length increased. All other morphological aspects were non-significant with the effect of body size removed (*P* >0.05).

4.2.6: Body condition Index (BCI)

Corpulence and condition index are important measures used in animal ecology that identify the parameters of body mass considered normal and healthy for a species (Green, 2001; Dudek et al. 2014); representative of an individual's fitness. Most importantly, they can be useful to detect trends of declining health in sample populations as response to disturbance (Gallego et al. 2016). A higher BCI score indicates a greater weight relative to length (overweight), whereas low scores could mean individuals are underweight. However, one concern with this method is that results tend to correlate with body size (Labocha et al. 2014).

Females had on average a lower mean score than males for BCI in 2017 (0.102 in male vs 0.098 in female), but that changed to a higher score in 2019 (0.090 in male vs 0.093 in female). The data both years was distributed normally (S-W 0.96 – 0.99, P >0.05). A t-test for equal means determined there was no significant difference in the BCI of males and females either year (2017: males N 117, females N 104, µ difference = 0.004, 95% conf. = -0.0003 0.009, t = 1.8435 (critical t = 1.9709), P (permutation) = >0.05; 2019: males N 59, females 74, µ difference = 0.003, 95% conf. = -0.0004 0.009, t = 0.7789 (1.9782), P = >0.05). That said, the same tests did detect a strong significant difference in male BCI between sample years (µ difference = 0.012, 95% conf. = 0.006 0.017, t = 4.4283 (1.9737), P = 0.0001), and a marginally significant difference in females (µ difference = 0.05, 95% conf. =-0.001 0.011, t = 2.7981 (1.9735), P= 0.051). That result suggests that mean BCI had decreased between sample years in both males and females, but the change was especially significant in male populations. This mirrors the significant and near significant results of the ANCOVA regressing SVL and weight (Figure 42); both results are representative of declining body condition.

In 2019, BCI may have decreased on average as a greater ratio of 'sub-adults' were sampled, and lizards of a smaller size tend to have smaller BCI. I did not remove sub-adult lizards from my analysis however, as the age classes I designated in the field were size-dependent, which is a highly speculative measurement of age based on the assumption that lizards grow continuously and at equal rates during their lifespan. Size is not always directly linked to age. Instead, the detected decrease in BCI may support the idea that a decline in the body size and relative health of *A. bicaorum* populations has occurred post disturbance, and that declining health and body condition may be an ongoing cause of decline.

The *A. bicaorum* sampled in 2019 may not have been explicitly younger in age, but rather smaller in size owing to changes in resource availability, and/or effects of declining intraspecific population density caused by disturbance. Alternatively, BCI may have declined because larger lizards have a greater susceptibility to predators, temperature/humidity fluctuations and other factors associated with disturbance that I did not measure.

To examine whether body condition interacted significantly with the morphology of either sex, I regressed relative dewlap size (dewlap length/SVL against body condition - Figure 43). I hypothesised that dewlap length might decrease with body condition (independent of SVL) between years, as lizards of lower body condition may have less energy to invest in dewlap development (Logan et al. 2012). Contrary to expectations, ANCOVA confirmed females had no significant difference in body condition ($F = 2.548$, $P = 0.1123$), but significantly greater dewlap lengths ($F = 29$, $P = 2.307E\text{-}07$). On the other hand, males significantly decreased in body condition ($F = 20.45$, $P = 1.133E\text{-}05$), but this had no impact on dewlap length relative to their body size ($F = 0.8588$ $P = 0.3554$).

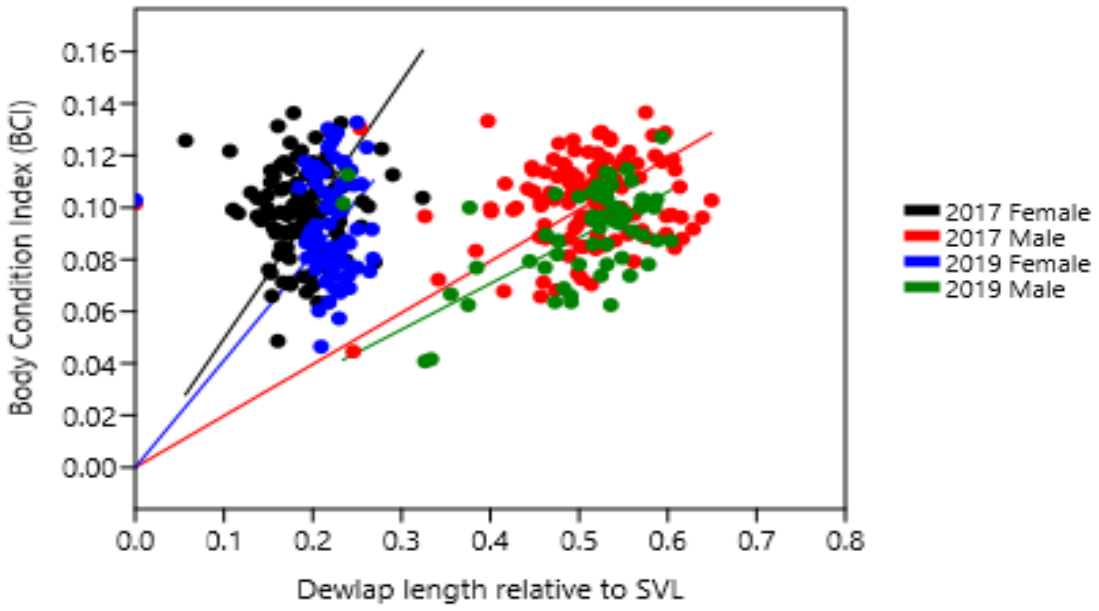


Figure 43. Linear models shows a regression of Body Condition (Mass/SVL) and relative dewlap size (Dewlap length/SVL) in both male and female *A. bicaorum*. Clear distinctions are seen between males and females and within each sex by year.

Variation in disturbance rate and intraspecific density among sample sites may explain this pattern. Female dewlaps may be under selective pressure to increase in length at lower population density, whereas in the same low-density post disturbance scenarios, males may respond with a decrease in SVL and relative body condition, which only affects their average dewlap length non-significantly by effect of reducing body size. As body condition did not decrease in both sexes alike, it seems unlikely declining body size is linked with a reduction in prey abundance. Considering the annual declines in abundance, density-dependence may be exerting a separate effect on the dewlap size and body condition of each sex independently, presumably via changes in competitive interactions (Calsbeek 2009; Logan et al. 2012).

4.2.7: Morphological change at each site between years

Using independent two-sample *t* tests (*p* values reported as Monte-Carlo permutation), a comparison of SVL by sex was performed to determine whether any detectable changes in populations within each site had occurred between years (Males - Table 20; Females – Table 21). Using the Bonferroni corrected alpha level of 0.0125, t-tests only identified significant declines in the mean SVL of males at site PH1 ($P = 0.0031$) and females at IB1 ($P = 0.0032$).

Table 20. The results of two-sample t-tests on male SVL (mm) separated by site and year.

Site	*Year*	*N*	*Mean* μ	*95% Conf.*	*Variance*	*Mean diff.*	*t*	*Critical t value*	*P =*
IB1	2017	27	65.3	63.4 67.2	23.183	-4.0	2.0689	2.0244	0.0437
	2019	13	61.3	57.1 65.6	50.423				
PH1	2017	22	68.4	66.8 69.9	11.421	-4.7	3.1529	2.0181	**0.0031**
	2019	22	63.7	60.9 66.4	37.656				
PH2	2017	50	64.7	63.4 66.1	22.499	-2.2	1.2679	1.999	0.2158
	2019	14	62.5	57.6 67.5	73.187				
PH3	2017	16	63.8	61.4 66.1	19.472	-0.5	0.26387	2.0739	0.8001
	2019	8	63.3	58.9 67.5	26.214				

Table 21. The results of two-sample t-tests on female SVL (mm) separated by site and year.

Site	*Year*	*N*	*Mean μ*	*95% Conf.*	*Variance*	*Mean diff.*	*t*	*Critical t value*	*P =*
IB1	2017	23	62.9	61.5 64.3	10.434	-3.6	3.0991	2.0227	**0.0032**
	2019	18	59.2	57.1 61.4	18.448				
PH1	2017	25	61.9	59.3 64.4	39.069	+1.1	0.63475	2.0086	0.528
	2019	27	63	60.4 65.6	44.037				
PH2	2017	36	60.5	58.9 62.1	21.507	-0.8	0.60539	2.0076	0.5514
	2019	17	59.6	57.1 62.3	26.493				
PH3	2017	12	61.4	59.0 63.8	14.304	+1.6	0.93153	2.0687	0.35991
	2019	13	63.1	60.1 66.1	23.744				

An ANCOVA using SVL as a covariate (Bonferroni corrected), detected significant annual differences in female dewlap length within every site except PH3 (Table 23). However, the same ANCOVA detected no significant annual difference in male dewlap length (P = 0.05), female (P = >0.05) or male body mass (P = >0.0125) independent of changes in SVL between sites – tables excluded.

Table 23. The results of ANCOVA comparing mean dewlap length (mm) of females at each site by year, adjusted using SVL as a covariate. Bonferroni corrected significance.

Site	*Year*	*N*	*Mean μ*	*Adjusted Mean*	*Mean diff.*	*F =*	*P =*
IB1	2017	23	11.4	11,2	+2	10.6	**0.0024**
	2019	18	12.9	13.2			
PH1	2017	25	11.6	11.8	+2.9	9.741	**0.0030**
	2019	27	14.9	14.7			
PH2	2017	36	11.1	11	+2.6	23.91	**<0.001**
	2019	17	13.5	13.6			
PH3	2017	12	14.4	14.5	-0.3	0.23	0.6363
	2019	13	14.3	14.2			

4.2.8: Relative density as a correlate of changes in sexual size dimorphism

I also examined changes in sexual size dimorphism across sites, which reflects the combined changes in male and female traits (Table 36). I hypothesised that variation in sexually dimorphic traits of morphology among sites each year may be density dependent, and therefore subject to influences of disturbance-driven declines in population size. For this analysis, I used the site estimates of relative density calculated from relative abundance (Schnabel index - Table 10); percentage changes in relative density correlated significantly with disturbance factors and overall were confirmed to be proportional to declines in true abundance (3.3).

All data was normally distributed (SVL: S-W 0.93, Dewlap: S-W 0.85, Body mass: S-W 0.95; Density: S-W 0.91, $P > 0.05$). Ordinary Least Squares Regression models were used to test for correlations between SSD (SVL) and relative population density (*A. bicaorum* per hectare) (Figure 44), as well as dimorphism in dewlap length (Figure 45) and body mass (Figure 46). Those results (fitted with 95% confidence limits) suggest a significant positive correlation between all measured factors of SSD, whereby sexually dimorphic differences in male-female morphology (especially dewlap size) are most pronounced at sites of high density (SVL: $r = 0.697$, $r^2 = 0.485$, $t = 2.38$, P (permutation) **= 0.05**; Dewlap Length: $r = 0.88$, $r^2 = 0.775$, $t = 4.54$, P = **<0.005**; Body mass: $r = 0.725$, $r^2 = 0.525$, $t = 2.58$, P = **<0.05**).

Table 24. Displaying the relative density (Schnabel index), male-female mean SVL, dewlap length (mm) and weight by sample site and year. Sexual Size Dimorphism (SSD) for SVL was calculated by dividing male-female values. Relative dewlap size (dewlap length/SVL) and weight (mass/SVL) was calculated to remove the effect of SVL prior to computing male-female ratios for dimorphism.

Site	*Year*	*Relative Density*	*Mean SVL*			*Relative Dewlap*			*Relative Weight*		
			Male	Female	SSD	Male	Female	Ratio	Male	Female	Ratio
IB1	2017	240	65.3	62.9	1.038	32.7	11.4	2.76	6.5	6.1	1.02
	2019	148	61.4	59.3	1.034	31.8	12.9	2.33	5.3	4.9	1.04
PH1	2017	188	68.4	61.9	1.105	36.6	11.6	2.85	7.5	6.2	1.12
	2019	54	63.7	63	1.010	33.6	14.1	2.22	5.9	6.4	0.92
PH2	2017	50	64.8	60.5	1.071	32.6	11.1	2.74	6.8	5.9	1.08
	2019	58	62.6	59.6	1.049	31.2	13.5	2.17	5.8	5.5	1
PH3	2017	121	63.8	61.4	1.038	32.4	14.4	2.17	6.1	6.2	0.95
	2019	108	63.3	63.1	1.003	32.8	14.3	2.28	5.7	6.3	0.91

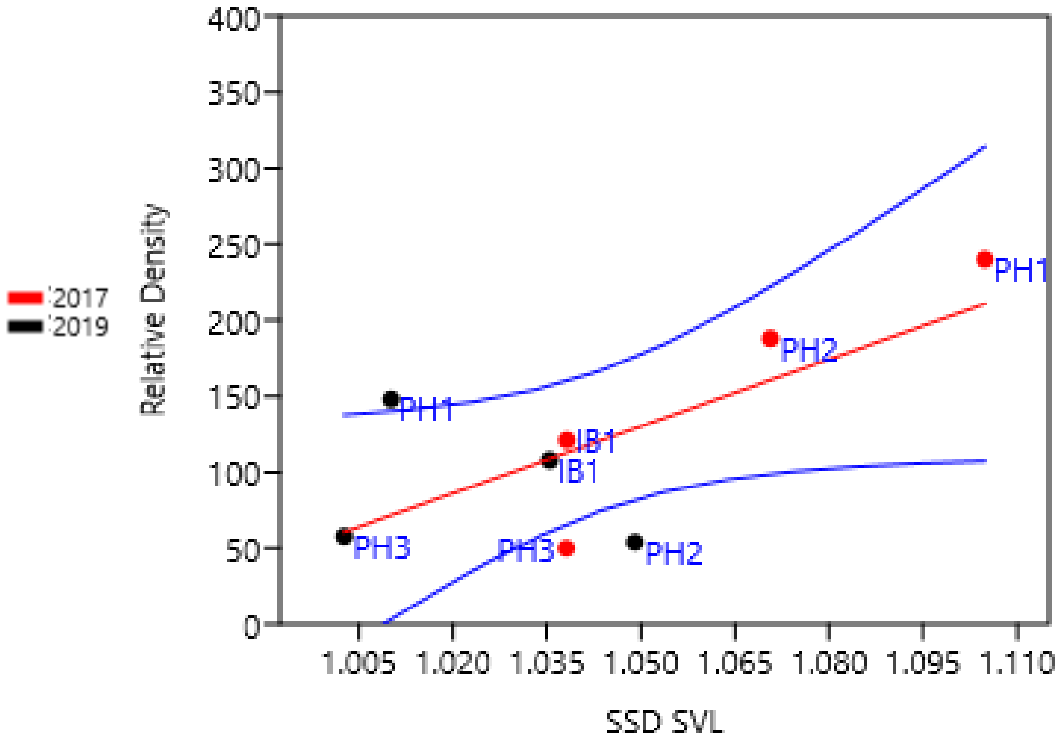


Figure 44. Regression model plotting SSD in SVL between sites and years. Male-bias SSD in SVL correlated significantly with greater relative density ($r = 0.697$, $r^2 = 0.485$, $t = 2.38$, $P =$ **0.05**)..

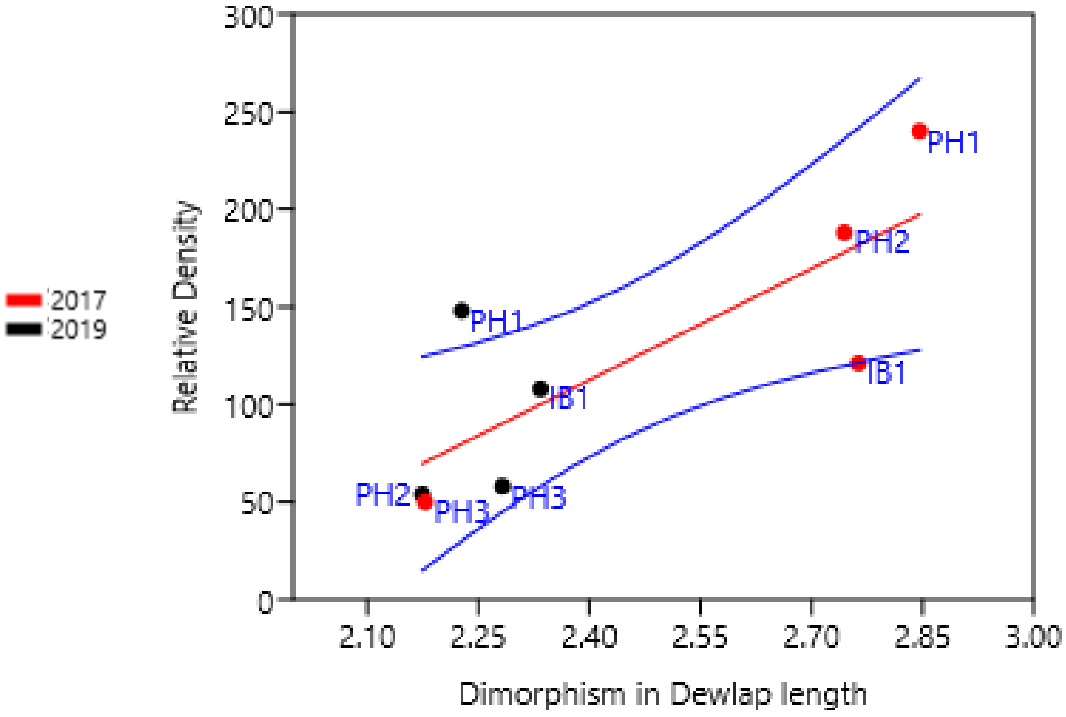


Figure 45. Regression model plotting dimorphism in dewlap length (mm) between sites and years. A significant positive correlation was detected with relative density (r = 0.88, r^2 = 0.775, t = 4.54, *P* = <**0.005**).

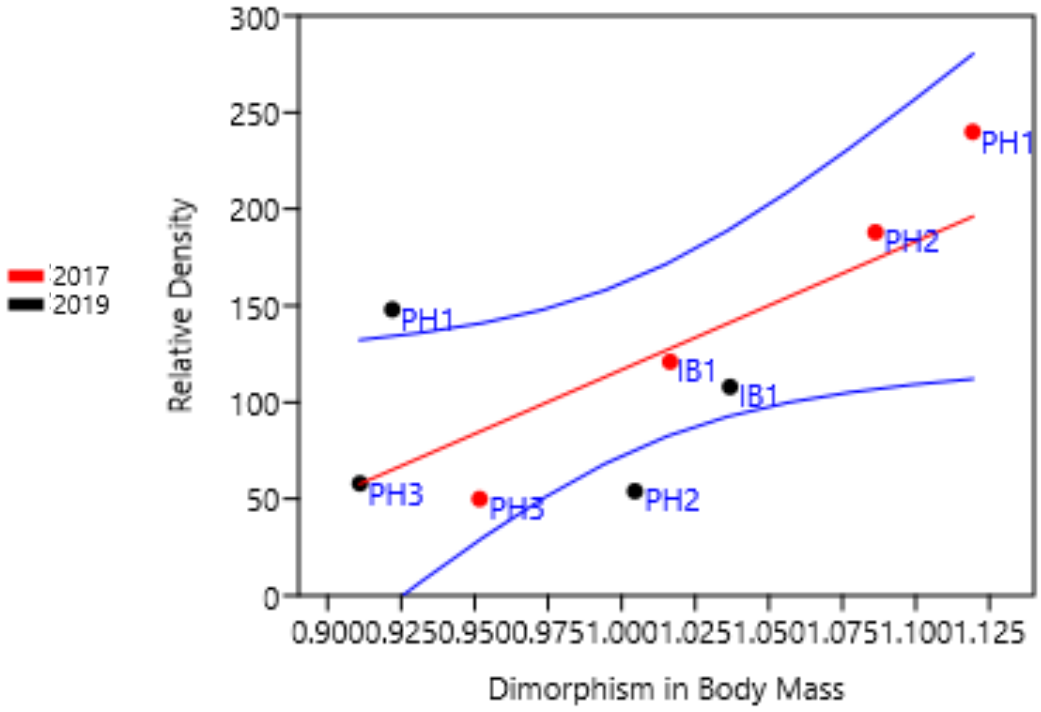


Figure 46. Body mass correlated significantly with relative density (r 0.725, r^2 0.525, t 2.58, *P* = <**0.05**).

4.3: Discussion

4.3.1: Do *A. bicaorum* exhibit sexually dimorphic traits in morphology?

My results on morphology have numerous implications regarding the current knowledge on *A. bicaorum* (4.2). McCranie & Kohler (2015) previously reported the SVL for the largest known female (86mm) and male (73mm) based on ten individuals of each sex, with averages of 66mm and 64mm respectively. The data I present increase the maximum-recorded size for male individuals, and contradict the suggestion that female *A. bicaorum* are predominantly larger than males. The maximum female SVL measurement of 86mm proposed by McCranie & Kohler (2015), might have been a typing error, given none of the 395 individuals sampled in my study were close to 80mm SVL. Moreover, earlier works in part by the same authors reported values more consistent with my results, stating female *A. bicaorum* reach a max SVL of 65mm, while males reach a max of 75mm (McCranie et al. 2005). Amid those inconsistencies, my data indicate with confidence that the maximum SVL of both males and females is somewhere between 70 - >80mm. The largest measured SVL in a female was 72mm, whereas the largest male was 76mm; which increases the maximum SVL known for both sexes (McCranie et al. 2005). Overall, *A. bicaorum* morphology seemingly follows the pattern of many anole species, having male-biased sexual size dimorphism in body size. (Fitch 1976; Butler & Losos 2002; Losos 2009).

4.3.2: Does *A. bicaorum* follow the same evolutionary pattern of sexual dimorphism as its relatives?

Anolis bicaorum exhibit male-bias sexual size dimorphism (4.2.1), but what are the wider implications of this on our knowledge regarding speciation and evolutionary divergence in the *A. lemurinus* sub-group? Given the surprising lack of quantitative morphological data on mainland *A. lemurinus*, the study of Logan et al. (2012) enables an important comparison, especially as the *A. lemurinus* populations on Cayos Cochinos are those from which *A. bicaorum* ancestrally stemmed (Klütsch et al. 2007). To recap, while those island *A. lemurinus* apparently differ in morphology and ecology from mainland *A. lemurinus* (Logan et al. 2012), Klütsch et al. (2007) found that populations in the Cayos Cochinos (Cayo Menor & Cayo Major) were genetically indistinguishable from one another and from mainland populations, suggesting that they have undergone limited evolutionary differentiation or that gene flow between them is ongoing. In contrast, *A. bicaorum* and *A. roatanensis* were both identifiable

from a unique set of genetic markers, indicating both had evolved under isolation for considerable time (Klütsch et al. 2007). Drawing comparisons from the relevant literature, it is immediately evident from my results that morphological differences exist between *A. lemurinus* and *A. bicaorum*, which suggest those species follow different patterns of sexual size dimorphism throughout their radiation. On Utila, sampled male *A. bicaorum* had on average a significantly greater SVL length than females (4.2.1; Figure 36). By contrast, female *A. lemurinus* on the mainland are demonstrated to have a larger maximum body size than males of up to 79mm (Savage 2002; D'Cruze & Stafford 2006; McCranie & Kohler 2015), but on Cayos Cochinos are shown to be relatively equal in body size (Logan et al. 2012).

Logan et al (2012) found no significant sexual dimorphism in the morphology of *A. lemurinus* on Cayos Cochinos (other than in dewlap); Males had an average SVL of 60-63mm, whereas females averaged 1mm longer, ranging from 61-64mm. Females body mass averaged from 5.4-6.4g, which was heavier than that in males (5.1-6g). However, tail length was slightly longer in males, averaging at 127-132mm vs 123-129 in females. In comparison to those results, my study found the SVL of male *A. bicaorum* averaged from 63-66mm, and females 61-62mm, with average weights of 5.7-6.7g and 5.7-6.1g respectively. Evidently, the body size of female *A. bicaorum* are similarly sized or smaller than female *A. lemurinus* on Cayos Cochinos, but male *A. bicaorum* by comparison to male *A. lemurinus* are approximately 3mm larger and nearly 0.7g heavier on average. Accounting for body size, results for both sexes of *A. bicaorum* suggest they have near equal average tail length (ratio: male 2.07; females 2.08) compared to their relatives on Cayos Cochinos (ratio to SVL: male 2.1; female 2.01 – Logan et al. 2012), though female *A. bicaorum* tails were longer than *A. lemurinus*.

The most pronounced of the morphological divergence between mainland, Cayos Cochinos *A. lemurinus* and Utila *A. bicaorum* island populations, is the apparent shift in dewlap length, whereby male and female *A. bicaorum* have adapted dewlaps of considerably greater size than *A. lemurinus*. Interestingly, Leenders (2019) reported that mainland *Anolis lemurinus* tend to occur in low density and that unlike other anole species in high-density populations, do not engage in male-male contests that involve dewlap displays. He also stated that the functional size of the female dewlap could sometimes lead to their misidentification as males, which infers that the sexual size dimorphism in their dewlap length is very small. The latter statement is supported by Savage (2002) and Guyer & Donnelly (2005); who also reported relatively equal dewlap size among sexes in mainland *A. lemurinus* (but neither stated measurements).

In contrast to the mainland, Logan et al. (2012) found male *A. lemurinus* dewlap length (DL) on Cayos Cochinos to be approximately three times larger than that of females; averages of 17-18mm in males (DL/SVL: 0.29), and 5mm in females (DL/SVL: 0.08). However, those dewlaps are still small compared to *A. bicaorum*; my study revealed that male *A. bicaorum* had average dewlap length (DL) of 31-33mm (DL/SVL = 0.5), whereas females averaged from 11-14mm (DL/SVL = 0.2). Dewlap length was the only feature that was scaled significantly different relative to body size. One similarity is that females of both island populations have a severely reduced dewlap size in comparison to their male counterparts (i.e. like *A. lemurinus* on Cayos Cochinos, male *A. bicaorum* dewlaps are also approximately three times larger than that of females). Nonetheless, *A. bicaorum* differ substantially from *A. lemurinus* on Cayos Cochinos (Logan et al. 2012), in that the dewlaps of both sexes averaged at around twice their length, and that male *A. bicaorum* reached a greater SVL than females. Unlike reports for *A. lemurinus* on the mainland (Leenders 2019), I frequently saw *A. bicaorum* display its dewlap and begin territorial disputes in high-density scenarios (Figure 47).

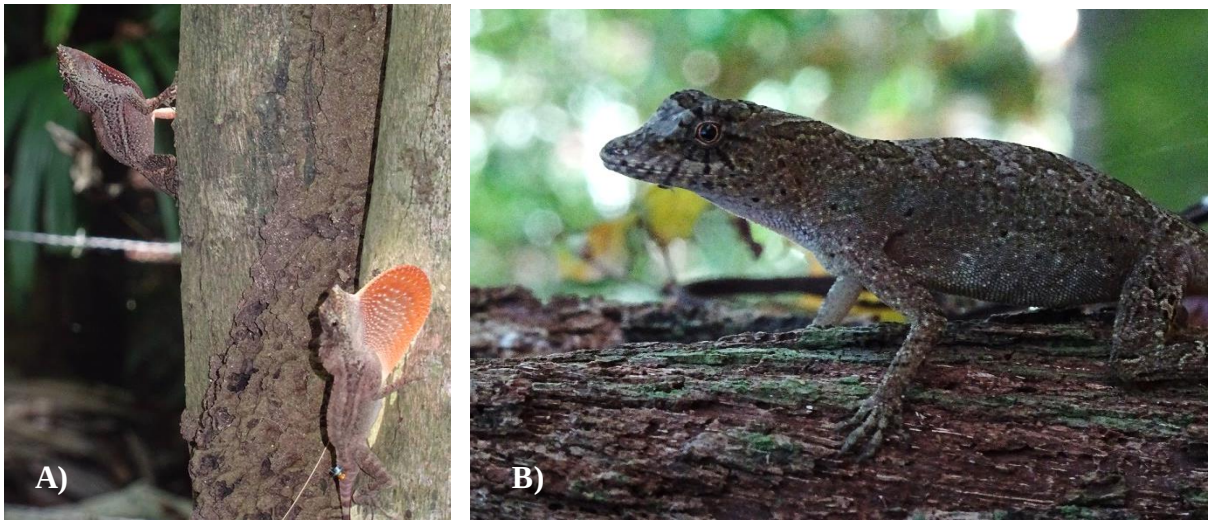


Figure 47. **(A):** Two male *A. bicaorum* engage in territorial confrontation; rivals will erect dorsal and nuchal crests while displaying their dewlaps. **(B):** A female *A. bicaorum* perched on a trunk in closed canopy broad-leaf forest.

Compared to the *A. lemurinus* studied by Logan et al (2012), for the most part my results show *A. bicaorum* to be larger morphologically in all measured aspects, most notably male SVL and the tail length and dewlap size of both sexes. This data therefore offers further validity to the description of *A. bicaorum* as a full species (Kohler 1996), with evidence for distinct morphological differences unlike those reported for the neighbouring *A. lemurinus* populations.

While not much information is available to include *A. roatanensis* for comparison, McCranie & Kohler (2015) reported their maximum SVL length at 65mm in males versus 62mm in females, with averages of 56mm and 58mm respectively; which would suggest *A. bicaorum* are considerably larger than their 'sister species' as well. Considering the morphological differences in the mainland, Cayos Cochinos and Utila populations, trends seem to indicate that *A. lemurinus* on Cayos Cochinos are living evidence of a transitory step in the switch of sexual size dimorphisms from larger female *A. lemurinus* on the mainland, to equal size on Cayos Cochinos, and now larger males in *A. bicaorum*. Males of *A. roatanensis* might also be larger than females as well, but that remains unclear from the small sample size of McCranie & Kohler (2015). As enlarged male features such as body and dewlap size enhance competitive ability during territorial disputes (Stamps & Krishnan 1994), consequently they should be under density-dependent natural selection (Calsbeek & Smith 2007). Considering the newly presented results on *A. bicaorum*, in accordance with Logan et al (2012), I confer that population density may be a key factor driving speciation and morphological divergence in the *A. lemurinus* group.

4.3.3: Does *A. bicaorum* morphology vary between hardwood forest sites and have disturbance-driven changes in density induced morphological responses in populations?

I compared the intra-annual variance in site morphology and combined differences among sites by year, and interpreted annual trends relative to disturbance-driven declines in abundance. The primary results concerning morphological variance between sites in 2017 was the detection of a significantly greater body size in males at the site of highest population density (PH1; Table 17 & 18), and a significantly greater dewlap length in females at the site of lowest density and pre-disturbance (PH3; Table 23). Interestingly, this trend of variance was no longer detectable in 2019 data, where instead there were no statistically significant differences in male or female morphology between any sites post disturbance.

The trend apparent from the Bonferroni corrected t-tests (Table 20 & 21) and ANCOVA results (Figure 40 & 41) is that site PH3 was the only site of no significant morphological variability between sample years. Though PH3 was a pre-disturbed site that exhibited the lowest density in 2017, in 2019, it exhibited the least change and was the site of most stable relative abundance/density due to a comparably lower-level of recent disturbance (Figure 32; Table 8 & 9). Males at site PH3 showed no significant difference in morphology between sample years; mean SVL remained equal to the nearest millimetre (Table 20). Females at PH3 also showed

no significant difference in morphology between years, but mean SVL increased slightly (Table 21), while dewlap length remained equal to the nearest mm (Table 23).

In contrast to PH3, sites that had been subject to high-levels of recent disturbance and correlative population declines between years, all had anole populations that exhibited significant annual differences in female dewlap length or male body size. This infers that the primary disturbance-driven response of declining density has a knock-on a secondary effect of spurring morphological change in anole populations, perhaps within a single generation.

Table 20; 21; 22 demonstrate that at site IB1, males did not vary in morphology between years, but female SVL decreased while their dewlap size significantly increased. At site PH1, males exhibited significant decreases in SVL, whereas female dewlap size increased significantly with non-significant increases in mean SVL. Males at site PH2 did not significantly change in morphology, however females demonstrated non-significant declines in SVL and significantly larger dewlaps. Considering the morphological results with reference to abundance estimates, I theorise that the primary cause of morphological differences among sites may be variation in the intraspecific population density, and the principal driver of annual shifts was declines in density relative to disturbance.

In females, an unsuspected trend was detected at all sites subject to disturbance-driven decline, which I interpret as a negative correlation of female dewlap size with high population density. In 2019, females at all sites except PH3, had significantly larger dewlap lengths (mm) than when originally sampled in 2017 (IB1 μ 11.2 +2, PH1 μ 11.8, +2.9, PH2 μ 11 +2.6; Table 23). At site IB1 & PH2, female dewlap length significantly increased even though their SVL decreased, reaffirming that a factor other than body size might be driving differences in female dewlap length. The effect of this was also seen in the regression of BCI and relative dewlap size (Figure 43).

By comparison to other sites, PH3 had the lowest anole density but the greatest female dewlap lengths in both years, and its annual sample means remained equal to the nearest millimetre (PH3 μ 14.5 -0.3). The prior ANCOVA analysed 2017 site differences in mean dewlap length, confirming that the dewlaps of PH3 females were significantly greater in size compared to females of all other sites (Figure 40 C). The formerly undisturbed sites had females with smaller sized dewlaps and equal SVL adjusted means of 11 to the nearest mm; no

significant differences were found between them. The result indicates that female dewlaps of all sites in 2019 had increased to become more analogous to those of PH3, and that less variance in dewlap length now occurs between sites as a whole (Figure 40 D & C; 41; Table 23).

As I considered PH3 to be the only post-disturbed site in 2017 with pre-existing evidence of human activity (see 3.1.1), it is safe to assume that *A. bicaorum* population declines may have occurred prior to my sampling. This assumption is appropriate, given that PH3 had by far the lowest observed anole density of any site both years.

Moreover, this assumption implies that the effect of my hypothesis regarding disturbance and a small population density on dewlap length at PH3 had already been detectable, and thus proposes a valid explanation as to why female dewlaps have been significantly larger at site PH3 since 2017, independent of their body size. Under this interpretation, the morphology of PH3 populations could be extrapolative of the low-density post-disturbance scenario that I find all other sampled populations are incipiently adapting towards. The lower density at PH3 need not link directly to disturbance, but may also be driven by relative habitat quality/suitability as a whole (for which I could not quantifiably test).

In 2017, site PH1 had the highest population density of all sampled sites that included those males exhibiting significantly greater SVL (Table 18). ANCOVA demonstrated males at PH1 only had significantly larger dewlap lengths in part to their greater body size, and no significant change was found in dewlap length independent of SVL (Figure 40 A). The results suggest that ecological conditions at PH1 (for some reason) resulted in males with an above average body size, and a higher density may explain this. Numerous untested factors could attribute to a larger body size and/or density at PH1, which include a greater prey abundance and faster growth rate, or perhaps lower predation rate and increased longevity.

Notably, detectability at site PH1 may have been biased by vegetation density and the difficult topography of the terrain (3.1.1), resulting in larger anoles being detected most easily. Despite difficult terrain however, PH1 did have the greatest CPUE and density estimate of any sample site (Table 5 & 10), therefore I maintain the terrain had little effect on my ability to detect lizards of any particular size at the site. Alternatively, I believe my data demonstrates that a high population density and the rate of intraspecific competition could drive proportionately larger males.

4.3.4: Is intraspecific population density a factor that drives sexual size dimorphism?

I have shown a significant correlation between population density and male-biased sexual size dimorphism in *A. bicaorum* body size, mass and dewlap length (Figure 44; 45; 46). SSD arises when the net effects of natural and sexual selection on body size differ between the sexes (Rohner et al. 2016). If population density is a reliable proxy for the intensity of intraspecific competition, this could mean that larger males are favoured due to their competitive advantage in zones of high population density, whereas males of a smaller average body size are outcompeted and disproportionately selected against. Given that weight and dewlap length in males is strongly correlated with SVL (Figure 37 & 39), proportionate reductions were also detected in those morphological features. However, declining density had the opposite effect on female dewlap length, whereby it increased in size at lower population density (independent of SVL length). This is demonstrated not only by the significant increase in female dewlap length across sites except PH3 (ANCOVA P = **<0.0125;** 4.2.5), but also in the annual regression of BCI with dewlap length (Figure 43), and the measure of dewlap SSD that significantly correlated with density (Figure 44).

One leading theory that potentially corresponds with our results for dewlap size is the pressure of social selection (i.e. male-female courtship and female-female territoriality). Using sexual size dimorphism as a proxy for male competition rates, Harrison & Poe (2012) predicted that female dewlap size should be negatively correlated with the degree of sexual size dimorphism. As male bias sexual size dimorphism is commonly linked to high competition rates in anoles (Vanhooydonck et al. 2005) (i.e. larger males have a competitive advantage against smaller rivals), it can be assumed that males engaging in high levels of interspecific competition for females will be less selective; consequently, the pressure driving elaborate ornamentation in females is reduced (Harrison & Poe 2012). Likewise, my results for *A. bicaorum* indicate that the ratio of sexual dimorphism in dewlap length decreased with declining density (Figure 44), for the most part due to female dewlaps getting larger independent of SVL rather than male dewlaps getting smaller.

Generally, in species that exhibit naturally skewed sex ratios, it is demonstrated that the more abundant sex will compete more for mating opportunities and thus be under stronger sexual selection (Kvarnemo & Ahnesjo, 1996). Distance sampling density estimates (post-stratified by sex) confirm that the operational sex ratio of male to female *A. bicaorum* within populations

did change between sample years, from more males in 2017 to more females in 2019 (Table 12); therefore, it is conceivable that factors driving sexual size dimorphism could be linked to competition rates within the predominant density of either sex (Emlen & Oring, 1977). However, my results (4.2) may only represent random fluctuations around a relatively equal sex ratio of 1:1, and such an interpretation would otherwise contradict a previous study of sexual selection in 14 different *Anolis* species, that found no evidence sex ratio bias is associated with sexual size dimorphism (Muralidhar & Johnson, 2017).

While male-bias traits may be sexually selected under high density, female morphology (i.e. dewlap size) "may be a fortuitously adaptive plastic response" to the newfound low-density degraded environment individuals now inhabit (Marnocha et al. 2011). Phenotypic plasticity (observed most commonly in plants – Gratani 2014) refers to non-genetic changes in an organism's behaviour, morphology or physiology, usually in response to environmental conditions. Mobile organisms (e.g. animals) can move when unfavourable conditions are presented, so consequently their long-term exposure to new environments and the requirement to adapt is often less intense. I cannot separate adaptive and plastic changes in my dataset. However, plasticity itself may be adaptive, allowing for flexibility in response to the environment (Ghalambor et al. 2007). Interspecific differences in anole morphology (e.g. ecomorphs) are widely considered to reflect adaptive change (Losos 2009), but anoles also show phenotypic plasticity within species.

Losos *et al.* (2000) raised captive *A. sagrei* in controlled environments while restricting individual access to different perch diameters; revealing that anoles with access to wider or thinner perches grew slightly longer or shorter legs; however, this plasticity could not fully account for differences in leg length among ectomorphs as observed on an adaptive or evolutionary scale. Likewise, I find that increasing female dewlap length cannot be fully explained by declines in population density if disturbance is assumed to have had equal effect on the density of both sexes, or if operational sex ratio has little independent effect of sexually dimorphic features (Muralidhar & Johnson, 2017). If the changes I observed in *A. bicaorum* are adaptive, or if plasticity itself is adaptive, this might indicate an influence of anthropogenic disturbance on their morphology and ecology that could have important implications on the evolutionary trajectory of this species (Marnocha et al. 2011).

As inferred by the six ecomorph classifications of Losos (2009), ecological divergence is a key factor driving the speciation of West Indian *Anolis* towards a predefined set of niches (Prelude), all of which occurred in the last c. 40 million years (Sherrett et al. 2015; Poe et al. 2017; McGlothlin et al. 2018). Supposing the 10,000-year-old radiation event of *A. lemurinus* across the Bay Islands remain in the early stages of speciation (Logan et al. 2012), rising anthropogenic pressures could impede on the natural ecological pressures driving a predictable future course of diversification and speciation in *A. bicaorum*. Ultimately, the continued long-term effects of anthropogenic change on Utila could either result in the precipitous decline and eventual extinction of *A. bicaorum*, or spur some form of human-induced adaptation and speciation in response to ecological changes (Bull & Maron, 2016).

5: Conclusions

The effects of population density are well-known to be a considerable force driving male-biased SSD, I suggest the associated natural pressures such as competition rates and social selection are factors driving the adaptation of a greater body and dewlap size in *A. bicaorum*. Given that male anoles are territorial, in high-density populations features such as a greater body and dewlap size may be increasingly vital for territorial maintenance and succeeding in confrontational interactions (Tokarz 1985; 2002). By this logic, males exhibiting greater body and dewlap size are more successful at defending a territory from rival males and assumedly also acquiring females. The effects of this can be seen in the results for *A. bicaorum* SSD, whereby male SVL, body mass and dewlap length was significantly above average at the site of highest density (Figure 44; 45; 46).

Evolutionarily speaking, this could be a leading explanation for why the Bay Islands members of the *A. lemurinus* complex (*A. bicaorum* & *A. roatanensis*) have diverged from their ancestors with considerably greater dewlap length (McCranie & Kohler 2015); because island anole density can exceed that which is possible on the mainland's more complex and fluctuant ecological scenario (i.e. with greater interspecific competition & predation rates). Unfortunately, I could find no quantitative literature on mainland or Cayos Cochinos *A. lemurinus* population density to further this hypothesis. Nor, is there any available information on *A. roatanensis* density. As such, I recommend this topic for future study.

My results suggest one possible morphological response of *A. bicaorum* to habitat degradation on Utila may be a reversal of the high density-dependent trend that initially drove the divergence of their enhanced sexually dimorphic traits. Quantitative SSD variation between taxa is common, but directional intraspecific SSD reversals are rare (Rohner et al. 2016) Significant annual changes in *A. bicaorum* morphology among sites likely represent an indirect secondary response to disturbance that is driven by the primary response of declining abundance and density. In effect, I hypothesise that disturbance-driven declines in density lead to a reduction in the level of interspecific competition that drives male-bias sexual size dimorphism in naturally unimpeded circumstances. Therefore, if current disturbance and declines in density continue on Utila, perhaps it can be expected that *A. bicaorum* of the future may not only be far less abundant in degraded habitats, but that males and females could lose the definition of their sexually dimorphic traits.

The exact mechanism behind these adaptive changes require further study, however, such may be induced by a reduction in male body size and condition, and an increase in female dewlap length. While a reduction in male size and condition seems an inevitable response to disturbance as well as low-density, the exact mechanism driving a greater female dewlap length in a disturbed low-density scenario is cryptic, and its adaptive benefits remains a topic for future investigation, but may be attributable to plasticity or differences in operational sex ratios.

My research concludes that habitat loss and degradation caused by numerous disturbance factors should be considered among the greatest threats to *A. bicaorum* abundance in hardwood forest, because these factors are significantly correlated with observed declines in abundance. The changes detected in sexually dimorphic traits of morphology (while not fully understood), indicate this species has the capacity to rapidly adapt its morphology in response to the disturbance-driven effect of lower density. As species morphology links closely to ecology (i.e. ecomorphs and ecomodes – Losos, 2009; Nicholson et al. 2012; 2018), my results infer that *A. bicaorum* may begin to change ecologically. However, as highlighted in 2.3.3, perhaps any hope that *A. bicaorum* could change its ecology and adapt to new-found degraded or urbanised habitats will be short-lived on an evolutionary timescale, considering that two readily-adaptable invasive species (*A. sagrei and A. allisoni*) are becoming established within disturbed regions and seem destined to compete for those niches once they are converted. The overall effects of habitat degradation, anthropogenic change and invasive species is likely to constrain, redirect or halt the future speciation of *A. bicaorum* within the *A. lemurinus* group. These long-

term effects are important to consider, as 'conservation biology is not only focused on conserving habitats, species richness or species in real time, but is about promoting evolutionary potential and processes at all levels of biodiversity' (Olivieri et al. 2016).

5.1: Conservation Status

"Anoles are known for many things, but conservation is not one of them" (Mahler & Castañeda, 2012). Despite the high rate of endemism present in the *Anolis* genus, the anthropogenic impacts of our changing world on many Caribbean and Neo-tropical species have yet to be evaluated. To date, only 117 (c. ¼) of the c. 427 *Anolis* have received IUCN Redlist species assessments (Uetz, 2019; IUCN, 2020), and only 19 of those are classed in an Endangered or Critically Endangered category.

Owing to the apparent versatility, high abundance and adaptability of some anoles, often the very concept of an *Anolis* threatened with extinction can be somewhat hard to swallow. Indeed, every species of anole will respond differently to unfavourable changes in its immediate environment. While generalist species such as *Anolis sagrei* are shown to thrive in a disturbed setting (Lapiedra et al. 2017; Tiatragul et al. 2017; Brown & Arrivillaga, 2017), others species that have adapted to specialise in a specific niche are shown to decline (Kolbe et al. 2016).

Of the 19 recognised highly threatened *Anolis* lizards, eight of them are forest dwelling species endemic to Caribbean islands (IUCN, 2020). For the most part, these cases of rapid population decline and extinction are linked to declining habitat quality on its own, or in combination with the arrival of invasive species. To name one example, the Culebra Island Giant Anole (*A. roosevelti*) is considered Critically Endangered (Possibly Extinct) by the IUCN Redlist (de Quiroz & Mayer, 2011), primarily owing to continued deforestation in its island range (Campbell & Dodd, 1982; Gaa Ojeda Kessler 2010).

While I acknowledge that my study lacks sufficient data across multiple years to indicate a continued population decline (3.3.2), my results are suggestive and a leading hypothesis must certainly be that *A. bicaorum* decline is directly linked with rising disturbance levels. Eighty percent of known wildlife extinctions have occurred on islands (Rickets et al. 2005), many of which have been endemic herpetofauna (Case et al. 1992). To prevent *A. bicaorum* joining that statistic, the apparent rapid decline of *A. bicaorum* need be taken seriously, and addressed with

continued study and monitoring of population trends to verify with certainty. While future research is required, it is my belief that *A. bicaorum* be considered as exceedingly vulnerable to the effects of habitat degradation, as the severity of the alleged decline should denote the necessity for pre-emptive conservation efforts sooner, rather than later.

Under current IUCN Redlist criteria for 'small population size and decline', *A. bicaorum* would certainly classify as Vulnerable C1, given the estimates number of mature individuals is >10,000, and apparent population declines of >25% have occurred within 3 years or one generation. However, when also accounting for its restricted 41km^2 (<100km^2) extent of occurrence, and even lower extent of occupancy (<10km^2), the overall data can warrant a much stronger classification. With that in mind, the information and observations I amassed during this study contained all the material needed to constitute the backbone of a well-informed IUCN assessment for *A. bicaorum*; that is collectively used to propose the species as Critically Endangered under IUCN criteria B1ab (i,ii,iii,v) + 2ab (i,ii,iii,v) (see Appendix 2). To date, only three *Anolis* are currently listed with Critically Endangered status (IUCN, 2020); hence, the proposed assessment for *A. bicaorum* places it among the world's most endangered anoles.

My study demonstrates via numerous methods that the dynamic and unique populations of the endemic *A. bicaorum* are significantly declining in their preferred habitat of hardwood forest, and perhaps even changing morphologically in response to disturbance, habitat altercation and the associated effects of declining density. The decline of *A. bicaorum* highlights the potential threat of ongoing and future impacts of deforestation and development on Utila. Unquestionably, continued study is needed to unveil the true extent to which *A. bicaorum* will be impacted by anthropogenic change, and indeed, whether they can adapt to survive in alternative habitats. While the trends of their declining abundance in degraded habitats fuel future concern for the species' conservation and longevity, the apparent morphological changes I detected in the remaining populations may be symbolic of an ecological response and means of coping with this change. It is with hope that my research will inform appropriate conservation action and form the baseline from which to monitor future changes in the ecology, abundance and morphology of *A. bicaorum*.

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Appendix 1: Supplementary Data

Table 3. Raw data for time-spent surveying in minutes. Four sites were surveyed. Each site contained 3 transects. This total of 12 transects were surveyed on 36 occasions (3 repeats per transect). Total time in minutes is shown for each transect and site. For ease of interpretation, occasions where search time increased in 2019 was highlighted in bold.

Site	*PH1 2017*			*PH2 2017*			*PH3 2017*			*IB1 2017*		
Transect	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	37	51	42	39	113	36	124	50	36	33	28	11
Day 2	16	54	129	33	59	82	133	78	41	43	51	34
Day 3	34	39	51	22	78	92	100	52	50	56	31	13
Total	87	144	222	94	250	210	357	180	127	132	110	58
Site Total		453			554			664			300	

Site	PH1 2019			PH2 2019			PH3 2019			IB1 2019		
Transect	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	**45**	42	29	**40**	40	**43**	92	**67**	**45**	**36**	**32**	**24**
Day 2	**52**	41	41	**35**	**61**	58	92	60	**60**	42	38	20
Day 3	**73**	**42**	37	**36**	51	48	93	**63**	**53**	36	30	**22**
Total	**170**	125	107	**111**	152	149	277	**190**	**158**	114	100	**66**
Site Total		402			412			625			280	

Table 4. Raw data for transect search speed in meters per minute (distance walked/time). For ease of comparison, 2019 transect speeds that decreased were highlighted bold (slower speed = greater search effort). Site average speed was calculated using the total survey time / total distance walked i.e. PH1 2017: 453/(150m x 9 = 1350m) = 2.98m walking speed per minute.

Site	*PH1 2017*			*PH2 2017*			*PH3 2017*			*IB1 2017*		
Transect	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	4	2.9	3.5	3.8	1.3	4.1	0.8	2	2.7	3	3.5	9
Day 2	9.3	2.7	1.1	4.5	2.5	1.8	0.7	1.2	2.4	2.3	1.9	2.9
Day 3	4.4	3.8	2.9	6.8	1.9	1.6	1	1.9	2	1.7	3.2	7.6
Transect Average	5.9	3.1	2.5	5	1.9	2.5	0.8	1.7	2.3	2.3	2.8	6.5
Site Average		3			2.4			2.7			3	

Site	PH1 2019			PH2 2019			PH3 2019			IB1 2019		
Transect	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	**3.3**	3.5	5.1	**3.7**	3.7	**3.4**	1	**1.4**	**2.2**	**2.7**	**3.1**	**4.1**
Day 2	**2.8**	3.6	3.6	**4.2**	**2.4**	2.5	1	1.6	**1.6**	**2.3**	2.6	5
Day 3	**2**	**3.5**	4	**4.1**	2.9	3.1	**1**	**1.5**	**1.8**	2.7	3.3	**4.5**
Transect Average	**2.7**	3.5	4.2	**4**	3	3	1	**1.5**	**1.9**	2.6	3	**4.5**
Site Average		3.4			3.3			2.9			3.2	

Table 6. Capture-Mark-Recapture data for each transect and site in its raw format, displaying the total quantity of captured, recaptured and new individuals. Four sites were surveyed, each site contained three transects. This total of twelve transects were surveyed on 36 occasions (3 x repeats per transect). For ease of comparison, 2019 capture rates that increased/remained equal are highlighted in bold. Encounter and capture rates were apparently higher in 2017.

Site/Year	**PH1 2017**									**PH1 2019**								
Data	Captures			Recaptures			New			Captures			Recaptures			New		
Transect	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	12	14	15	-	-	-	12	14	15	9	10	6	-	-	-	9	10	6
Day 2	14	25	38	6	3	5	8	22	33	12	7	8	4	**4**	0	**8**	3	8
Day 3	15	19	25	11	8	10	4	11	15	8	10	6	4	1	0	**4**	9	6
Total	42	60	81	18	13	18	25	49	66	30	29	23	9	7	3	22	24	23
Site Total	177			43			134			76			13			63		

Site/Year	**PH2 2017**									**PH2 2019**								
Data	Captures			Recaptures			New			Captures			Recaptures			New		
Transect	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	11	32	12	-	-	-	11	32	12	2	7	6	-	-	-	2	7	6
Day 2	9	18	26	3	7	5	6	11	21	4	7	11	1	3	2	3	4	9
Day 3	5	22	20	5	16	7	0	6	14	4	6	9	3	3	**7**	**1**	3	2
Total	25	72	58	8	23	12	17	49	47	10	20	26	4	6	9	6	14	17
Site Total	155			43			113			56			19			37		

Site/Year	**PH3 2017**									**PH3 2019**								
Data	Captures			Recaptures			New			Captures			Recaptures			New		
Transect	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	15	4	0	-	-	-	15	4	0	8	**4**	**0**	-	-	-	8	**4**	**0**
Day 2	13	5	0	11	1	0	2	4	0	8	**6**	**5**	3	**3**	**1**	5	3	**4**
Day 3	17	6	0	15	4	0	2	2	0	8	3	**4**	6	3	**1**	2	0	**3**
Total	45	15	0	26	5	0	19	10	0	24	13	**9**	9	**6**	**2**	15	7	**7**
Site Total	60			31			29			46			17			**29**		

Site/Year	**IB1 2017**									**IB1 2019**								
Data	Captures			Recaptures			New			Captures			Recaptures			New		
Transect	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Day 1	6	7	1	-	-	-	6	7	1	**9**	**8**	**1**	-	-	-	**9**	**8**	**1**
Day 2	13	14	5	4	2	1	9	12	4	10	9	2	3	**2**	**1**	7	7	1
Day 3	20	13	2	9	7	2	11	6	0	5	5	**2**	1	3	**2**	4	2	0
Total	39	34	8	13	9	3	26	25	5	24	22	5	4	5	**3**	20	17	2
Site Total	81			25			56			51			12			39		

Table 7. Summary of recapture rates according to the sample site, year and the sex of *A. bicaorum*. Individuals never recaptured, excluded any new individuals caught on the final survey occasion.

Site	Year	Individuals recaptured on ≥1 occasion		Individuals never recaptured		Percentage recaptured	
		Male	Female	Male	Female	Male	Female
IB1	2017	8	10	9	6	0.47	0.63
	2019	4	6	8	10	0.33	0.38
PH1	2017	11	16	12	14	0.48	0.53
	2019	8	3	10	21	0.44	0.13
PH2	2017	23	14	23	22	0.50	0.39
	2019	10	9	2	8	0.83	0.53
PH3	2017	11	11	5	1	0.69	0.92
	2019	7	12	5	3	0.47	0.63

Appendix 2: IUCN Redlist Assessment for *Anolis bicaorum*

Higher Taxonomic Details:

Kingdom	Phylum	Class	Order	Family
Animalia	Chordata	Reptilia	Squamata	Dactyloidae

Taxon name: *Anolis bicaorum* (Kohler, 1996)

Synonym: *Norops bicaorum* (Kohler, 1996)

Common Name: Bica Anole

Etymology – Named in honour of the Bay Islands Conservation Association (BICA).



Species Photograph: Adult male (*A. bicaorum*) engaged in dewlap display (© T.W. Brown)

Taxonomic Notes:

Nicholson et al. (2012; 2018) most recently proposed the recognition of multiple anoline genera (considered subgenera or clades within the "crown clade" *Anolis*; e.g., Poe et al. 2017). Among these is the genus *Norops*, to which the species *Anolis bicaorum* was originally assigned (Kohler, 1996). *Anolis bicaorum* belongs to the *Anolis lemurinus* species sub-group (McCranie & Kohler, 2015) within the *Anolis auratus* sub-clade (Nicholson et al. 2012). The closest relative of *A. bicaorum* is its sister species *Anolis roatanensis*, which is endemic to the neighbouring island of Roatan (Kohler & McCranie, 2001), both relatives of *A. lemurinus* that is widespread in mainland Central America and present on Cayos Cochinos (McCranie & Kohler, 2015). A stepping stone model of island colonisation and evolutionary radiation was proposed for these species, with the Bay Island populations deriving from *A. lemurinus* on mainland Honduras, colonising Cayos Cochinos (*A. lemurinus*) before Utila (*A. bicaorum*) and Roatan (*A. roatanensis*) independently (Klütsch et al. 2007; Logan et al. 2012).

Current Assessment

Red List Category & Criteria: Critically Endangered B1ab (i,ii,iii,v) + 2ab (i,ii,iii,v)

Year Published: 2020

Date Assessed: December 2, 2019

Assessors:

Brown, T. W., Higgins, E., Algar, A.C., Owen, S.

Contributors:

Maryon, D.F., Ardon, D., Diotallevi, F., Martinez, A., Clayson, S.

Evaluators:

N/A

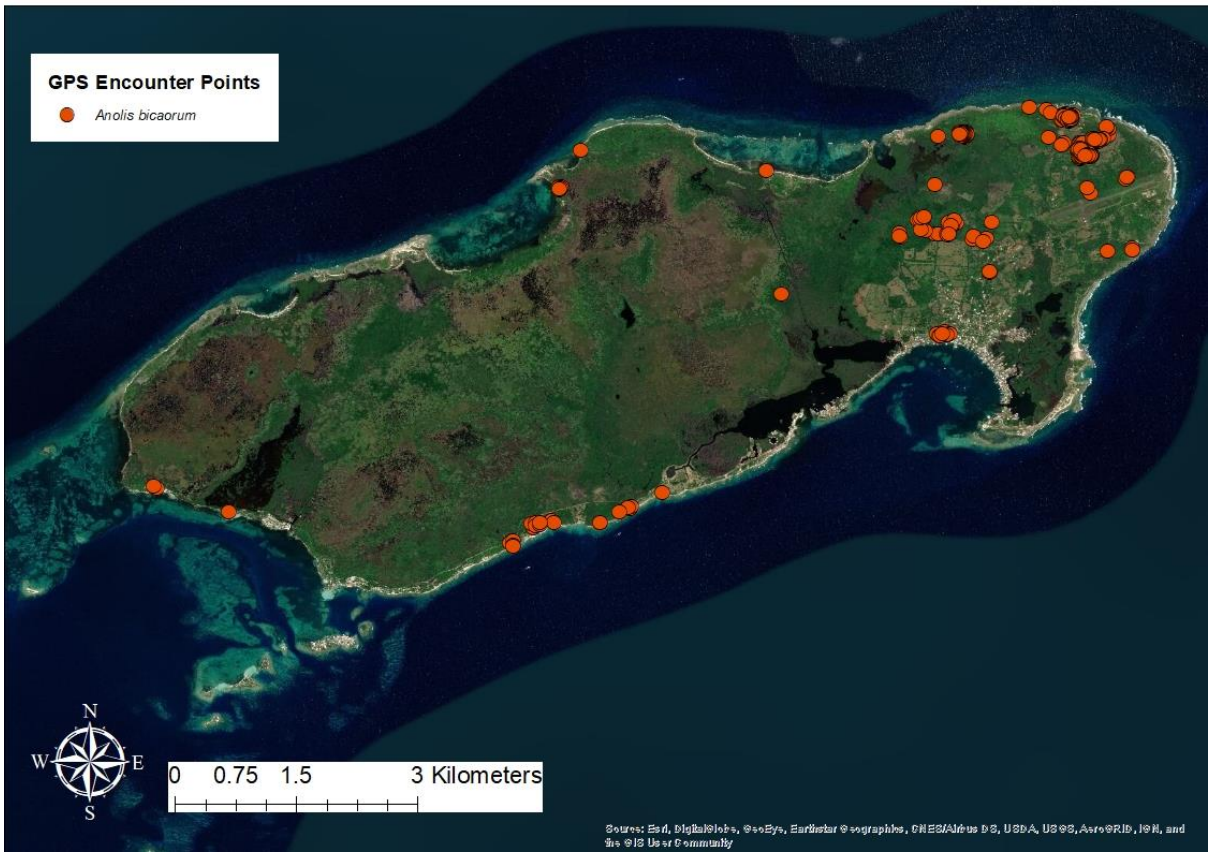
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Justification:

Anolis bicaorum is endemic to Isla de Utila, Honduras, The species is classified as Critically Endangered in accordance with IUCN criteria, as its total extent of occurrence is limited to the islands 41km^2 territory (B1a: EOO >100km^2), and its area of occupancy is restricted to an approximate 3.45km^2 of suitable forest habitat on Utila (B2a: AOO <10km^2). From 2017 – 2019, observations suggest a reduction in the 3.45km^2 forest cover has since occurred (B1 +2b[i,ii,iii]). Preliminary research during that same timespan estimated average adult population declines of >50% within monitored areas (B1+2b[v]), demonstrating that *A. bicaorum* are highly vulnerable to habitat disturbance. While land use change and deforestation is the primary threat driving *A. bicaorum* decline, future threats also include the establishment and spread of invasive anoles *Anolis sagrei* and *Anolis allisoni*. Continued population monitoring is needed to track further changes in conservation status, habitat quality and to better understand the interactions of endemic and invasive species.

Geographic Range Information:

Anolis bicaorum is known only from Isla de Utila, located in the Honduran department of Islas de la Bahía. Utila Island is the westernmost of the three major Bay Islands and neighbour to the Cayos Cochinos archipelago (McCranie et al., 2005). The species extent of occurrence (EOO) is restricted to the islands surface area of 41 km² from sea level up to 74m asl. Its area of occupancy (AOO) is restricted to <10km^2. A 2017 land cover map by Maryon (2020) classifies and estimates the areas of hardwood forest habitat available for *A. bicaorum* at 3.45km². Literature states *A. bicaorum* populations are distributed mostly within forest habitats on the eastern side of the island (McCranie & Kohler 2015). Island wide surveys have also detected disjointed populations within limited areas of coastal forest on the northern, southern and western shorelines (Brown et al. 2017a). GPS encounter points collected for *A. bicaorum* from 2017-2019 are plotted to represent the known distribution and area of occupancy.



Distribution map: GPS encounter points for *A. bicaorum* on Utila Island (2016-2019)

Range Countries

Honduras > Isla de Utila (Native)

Regions Possibly Extinct, Introduced, or Presence Uncertain:

None: the species is endemic to Utila Island, Honduras; and to our knowledge has not been introduced elsewhere nor does it occur on other neighbouring small islands/cays.

Population Information

McCranie & Kohler (2015) suggested that *A. bicaorum* be classified as Near Threatened in accordance with IUCN criteria, stating that their populations were declining in altered habitat. In accord, Johnson et al. (2015) placed *A. bicaorum* in the middle portion of the high vulnerability category in a conservation reassessment of Central American Herpetofauna, calculating an environmental vulnerability score of 17 out of 20. In 2017 & 2019, Capture-mark-recapture (CMR) studies (a collaboration between local NGO Kanahau Utila Research & Conservation Facility [KURCF] and the University of Nottingham, UK [UON]) have monitored the populations of *A. bicaorum* at forest sites in the eastern region. Four sites (2 x 0.9ha; 2 x 0.6ha) were sampled and resurveyed with consistent effort, to identify the ecological response of populations to disturbance. As a whole, the study recorded and collected morphological data on 395 individual (192 male: 195 female). Approximately 75% (2017 = 81.5%; 2019 = 63.4%) of individuals in the sampled population were mature adults (>60mm SVL), and a sex ratio of 98 males per every 100 females (2017 = 109:100; 2019 = 79.7:100) was obtained. The abundance of *A. bicaorum* varied between forest habitats of different types and quality. The highest density per hectare was in pristine mature hardwood and palm forest habitat. Combining the CMR results of all forest sites by year, the absolute density estimate produced using distance sampling for *A. bicaorum* within forest habitat was 285 (156-521) individuals per hectare in 2017, which had declined to 138 (68-280) individuals per hectare by 2019. Using the predicted 3.45km^2 of suitable forest habitat characterised by the 2017 Utila land cover map (Maryon, 2020), density estimates were extrapolated to obtain an estimation of *A. bicaorum* total island abundance (98,444 in 2017, dropping to 47,483 in 2019). The results indicated an overall >50% decline of *A. bicaorum* populations between sample years. Three of four sample sites monitored in 2017 & 2019 exhibited disturbance driven population declines of between 10 – 75%. Although many population dynamics need further research, initial evidence infers *A. bicaorum* populations are Critically Endangered as they could exhibit a rapid decline in response to continued degradation of Utila's forest habitat.

Population trend:

Decreasing

Habitat and Ecology

Anolis bicaorum has been observed using various habitat types on the island, ranging from preferred old growth broad-leaf/palm forest to secondary forest, coastal forest, white mangrove (*Laguncularia racemosa*), and disturbed areas such as gardens and vegetated agricultural fringes/fence rows. Their preferred habitat and zone of highest population density is within lowland tropical hardwood forest with dense understories consisting of mature vines, saplings and palms. The abundance of *A. bicaorum* in such forest interiors contrasts their relative absence among other habitat types. In Utila's tropical forests, it is common to find *A. bicaorum* active throughout the day on the trunks of trees and while they sleep at night on palm fronds. Many elements of their natural history have been documented, including descriptions of behaviour, habitat use, and diurnal/nocturnal ecology (Brown et al. 2017a). Niche partitioning is reported in forest habitats between *A. bicaorum* and its insular endemic congener *Anolis utilensis* (Brown et al. 2017b). Owing to their size and the relative lack of sympatric competitors (i.e. *A. utilensis* is smaller and inhabits a strictly canopy niche), *A. bicaorum* is active among and capable of exploiting many layers within the forest structure, from leaf-litter to upwards of 5m into the canopy. However, the most common perch height observed was between 1 - 2m high on the sides of tree/palm trunks. Both males and females are typically encountered in a vertical downwards facing position, as this positioning facilitates the ambushing of invertebrate prey on the leaf-litter (Brown et al. 2017a). A commonly observed component of their diet is spiders of the families Lycosidae and Salticidae. Males typically perch higher than females, presumably as communication via dewlap demands that individuals display from an optimum point of visibility. Observations of marked individuals spanning 6-12 months demonstrated males and females each occupy a small territory and home range of 5 – 10m^2 (Brown, 2019).

Morphology:

Analysis of morphological data collected during the 2017 & 2019 population study by KURCF and UON, found males to be larger than females in all measured aspects of morphology (T. Brown per.observ). Summary of male-female data as follows; SVL size (mm): [2017 = 63mm (45-76mm) in males vs 61.3mm (43-70mm) in females; 2019 = 65.5mm (45-75mm) in males vs 62mm (41-72) in females]; Body mass (g): [2017 = 6.7 (2-9.4) in males vs 6.1 (2-8.8) in females; 2019 = 5.78 (2-8.5) in males vs 5.77 (2-9) in females]; Dewlap size (mm): [2017 = 33.3 (11 – 44) in males vs 11.7 (4 – 21) in females; 2019 = 31.2 (15-41) in males vs 13.7 (9-18) in females]; Tail length (mm): [2017 = 135.5mm (105 - 161mm) in males and 128.4mm

(106-157mm) in females; 2019 = 130.9mm (91-156mm) in males and 128.4 (92-151mm) in females]. Males exhibit a large brick-red dewlap c. 2.8 x larger than that of females. Results indicate the colour of female dewlaps transition from red, pink to white with relative maturity (White et al. 2019; Brown, T pers.observ). Tail break frequency occurred at relatively equal rates in both males and females between sample years. Overall, tail loss and/or regrowth was present in 25-30% of the sampled population, which could represent the natural predation or intraspecific competition rates.

Reproduction:

Anolis bicaorum is oviparous and assumed to breed all year round given the correct environmental conditions. However, breeding may be restricted to the dry season, as hatchlings and reproduction is only recorded between February – September (Brown et al. 2017a). Copulation occurs on sturdy perches (e.g. branches, mature vines etc.) typically >1m above ground. No data on in-situ nest sites is available. In captive populations, females deposit a single egg in the leaf-litter every 15 days (Van Beest & Hartman, 2003).

Threat Information

Habitat loss:

The principal threat to this anole is habitat loss owing to the sale, deforestation and development of hardwood and palm forest habitats on Utila. Core populations in the northeastern region are increasingly impacted by the encroachment of agriculture and development. Deforestation is directly attributable to expanding agriculture and land development. Hardwood forest habitats are accessible and regularly poached for lumber, or have understory vegetation cut back during maintenance or for aesthetics prior to sale. Evidence demonstrates that forest cover has declined 2017-2019, and the current rate will likely continue into the future.

Invasive species:

A second major concern is the introduction and establishment of the notoriously invasive Brown Anole (*Anolis sagrei*). Given *A. sagrei* is well adapted to urban environments, the range of this invader could increase exponentially in synergism with island development. Currently

A. sagrei is well established and hugely abundant throughout Utila Town, and has dispersed a >1.5km radius from its presumed initial point of introduction (at Utila Ferry Port); occupying gardens, coastal forest and mangrove habitat. As primary forest habitats are further encroached upon, degraded and generally closer to human settlements, it is anticipated that *A. sagrei* could compete with *A. bicaorum* in its natural habitat. The recent introduction and establishment of a second anole species *A. allisoni* on Utila could add further complications. However, in comparison to *A. sagrei*, we do not consider *A. allisoni* a significant threat to *A. bicaorum*, as *A. allisoni* is native to the neighbouring Isla de Roatan and sympatric with the sister species of *A. bicaorum* i.e. *A. roatanensis*. Nonetheless, the growing establishment of new anole competitors could incur dynamic future ecological shifts that overall disadvantage endemic anole communities on Utila.

Predators:

Few native predators of *A. bicaorum* have been observed, though these anoles likely feature in the diet of snakes such as the Salmon-bellied Racer (*Mastigodryas melanolomus*), Mexican Parrot Snake (*Leptophis mexicanus*), Brown Vine Snake (*Oxybelis aeneus*), Green Vine Snake (*Oxybelis fulgidus* – Brown et al. 2019) and predatory lizards such as Brown Basilisk (*Basiliscus vittatus)* and Common spiny-tailed Iguana (*Ctenosaura similis*). This anole also appears easy prey for birds such as Great-tailed Grackle (*Quiscalus mexicanus*). Introduced predators such as domestic cats are free roaming on Utila and pose a local predation risk.

Use and Trade

There are no apparent pressures from collection, hunting, illegal use and trade of this species. To our knowledge, there are no populations of this species currently held in captivity.

Conservation Measures

Research led by local NGO Kanahau Research & Conservation Facility (KURCF) with the collaboration and support of the University of Nottingham (UON), will continue standardised abundance monitoring to track annual changes in the status of populations while collecting ecological and morphological data. Additionally, *A. bicaorum* is the focus of a PhD project at UON using pioneering techniques such as remote sensing to predict habitat suitability (Higgins, pers.comm) To date, conservation research by KURCF & UON has received support and

funding from the Mohammed bin Zayed Conservation Fund (project #172515600 – Brown, 2017). Additional research includes an on-going collaboration between the University of Harvard, US (UOH) and KURCF to investigate morphological variation in *A. bicaorum* by comparison to other relatives in the widespread *A. lemurinus* group (e.g. White et al. 2019). Future research recommendations include: 1) continued standardised monitoring of population status and habitat degradation trends; 2) further investigation of *N. bicaorum* abundance, behaviour, ecology and natural history; 3) assessment and monitoring of invasive *A. sagrei* populations/ frontline interactions with *A. bicaorum*.

Recommended conservation measures include developing active management schemes to protect anole populations and their habitats. While recognised as an essential habitat for biodiversity, currently no areas of Hardwood forest have been designated for conservation or protection on Utila. The only designated protected area (Turtle Harbour Wildlife Refuge) contains less than 0.5km^2 of suitable forest habitat for *A. bicaorum*, and only a small population (<10 individuals) have ever been observed within its boundaries. Any proposed designations for new protected areas should include areas of mature broad-leaf forest with an existing high *A. bicaorum* density. Priority conservation zones for *A. bicaorum* include the unique primary forests that remain in the regions of Pumpkin Hill, Ironbound and Jerico. A potential action might be to collaborate with landowners and/or purchase areas of forest habitat to create private wildlife reserves, protect a network of biological corridors and restrict unsustainable forest practices. Any pledge to conserve key forest habitat with local stakeholders and authorities must be agreed soon, as the current development pace has already affected these ecosystems.

Additional conservation actions should include environmental education and engagement with both the local community and tourists about the endemic anole populations and the importance of forest ecosystems, as recognition and appreciation is crucial for the species' long-term survival (e.g. Brown, 2018). Local initiatives and NGO's should highlight the Critically Endangered and endemic status of *A. bicaorum*, as well as exploring the potential environmental and economic incentives for landowners protecting its forest habitat. Information boards should be placed in key public-accessed forest habitats and in town, providing facts regarding *Anolis bicaorum*, threats, its conservation status and how to minimise human impact. Such a sign should encourage simple lizard friendly practices, e.g. advising against harvesting understory palm leaves and lumber from within forest habitats, and discourage the raking of leaf-litter in forested coastal habitats and gardens.

Habitats
(http://www.iucnredlist.org/technical-documents/classification-schemes)

Habitat	Season	Suitability	Major Importance?
1. Forest -> 1.6. Forest – Subtropical/Tropical Moist Lowland	Resident/ Breeding	Suitable	Yes
1. Forest -> 1.7. Forest - Subtropical/Tropical Mangrove Vegetation Above High Tide Level	Unknown	Marginal	-
1. Forest -> 1.8. Forest - Subtropical/Tropical Swamp	Unknown	Marginal	-
14. Artificial/Terrestrial -> 14.4. Artificial/Terrestrial - Rural Gardens	Resident	Marginal	-
14. Artificial/Terrestrial -> 14.6 Subtropical/Tropical Heavily Degraded Former Forest	Unknown	Marginal	-

Threats
(http://www.iucnredlist.org/technical-documents/classification-schemes)

Threats	Timing	Scope	Severity	Impact Score
1. Residential & commercial development -> 1.1. Housing & urban areas	Ongoing	Unknown	Likely to cause rapid declines	Unknown
Stresses:		1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
1. Residential & commercial development -> 1.2. Commercial & industrial areas	Ongoing	Unknown	Likely to cause rapid declines	Unknown
Stresses:		1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
1. Residential & commercial development -> 1.3. Tourism & recreation areas	Ongoing	Unknown	Likely to cause rapid declines	Unknown
Stresses:		1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
2. Agriculture & aquaculture -> 2.1. Annual & perennial non-timber crops -> 2.1.2. Small-holder farming	Ongoing	Unknown	Likely to cause rapid declines	Unknown
Stresses:		1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
2. Agriculture & aquaculture -> 2.3 Livestock Farming & Ranching -> 2.3.2. Small-holder Grazing, Ranching or Farming	Ongoing	Unknown	Likely to cause rapid declines	Unknown
Stresses:		1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
4. Transportation & service corridors -> 4.1. Roads & railroads	Ongoing	<50%	Likely to cause negligible decline	Unknown
Stresses:		1. Ecosystem stresses -> 1.2. Ecosystem degradation 1. Ecosystem stresses -> 1.3. Indirect ecosystem effects		

5. Biological Resource Use -> 5.2 Gathering Terrestrial Plants -> 5.2.2 Unintentional effects (species being assessed is not the target) -> collection of palm leaves for thatch-roofing projects	Ongoing	Unknown	Causing/could cause fluctuation	Unknown
	Stresses:	1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
5. Biological Resource Use -> 5.3 Logging & Wood Harvesting -> 5.3.3 Unintentional effects: subsistence/small scale (species being assessed is not the target) [harvest]	Ongoing	Unknown	Likely to cause rapid declines	Unknown
	Stresses:	1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.2. Ecosystem degradation2. 2. Species stresses -> 2.2. Species disturbance		
6. Human Intrusions & Disturbance -> 6.1 Recreational activities -> Increasing human traffic associated with tourism	Ongoing	Unknown	Slow, but significant decline	Unknown
	Stresses:	1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
6. Human Intrusions & Disturbance -> 6.3 Work & Other Activities -> Construction, development and agricultural work	Ongoing	Unknown	Likely to cause rapid declines	Unknown
	Stresses:	1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
7. Natural system modifications -> 7.3. Other ecosystem modifications -> Land maintenance (cutting, burning, removing vegetation; raking leaf-litter; collecting palm leaves)	Ongoing	Unknown	Likely to cause rapid declines clines	Unknown
	Stresses:	1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
8. Invasive and other problematic species, genes & diseases -> 8.1. Invasive non-native/alien species/diseases -> 8.1.2. Named species (*Felis catus* and *Anolis sagrei*/*Anolis allisoni;*)	Ongoing	Unknown	Causing/could cause fluctuation	Unknown
	Stresses:	2. Species stresses -> 2.1. Species mortality -> (*Felis catus*) 2. Species stresses -> 2.3. Indirect Species Effects -> 2.3.2. Competition -> (Introduced *Anolis* sp.)		
9. Pollution -> 9.4. Garbage & solid waste -> Plastic and municipal waste	Ongoing	<50%	Unknown	Unknown
	Stresses:	1. Ecosystem stresses -> 1.2. Ecosystem degradation 2. Species stresses -> 2.2. Species disturbance		
11. Climate change & severe weather -> 11.1. Habitat shifting & alteration	Ongoing	<90%	Causing/could cause fluctuation	Unknown
	Stresses:	1. Ecosystem stresses -> 1.1. Ecosystem conversion 1. Ecosystem stresses -> 1.3 Indirect ecosystem effects		

Conservation Actions in Place
(http://www.iucnredlist.org/technical-documents/classification-schemes)

Conservation Actions in Place
In-Place Research, Monitoring and Planning
Action Recovery plan: No
Systematic monitoring scheme: Yes
In-Place Land/Water Protection and Management
Conservation sites identified: Yes, over small part of range
Occur in at least one PA: Yes
Area based regional management plan: Unknown
Invasive species control or prevention: No
In-Place Species Management
Harvest management plan: No
Successfully reintroduced or introduced benignly: No
Subject to ex-situ conservation: No
In-Place Education
Subject to recent education and awareness programmes: Yes
Included in international legislation: Unknown
Subject to any international management/trade controls: Unknown

Conservation Actions Needed
(http://www.iucnredlist.org/technical-documents/classification-schemes)

Conservation Actions Needed
1. Land/water protection -> 1.1. Site/area protection -> designate forest reserves
1. Land/water protection -> 1.2. Resource & habitat protection -> private reserves
2. Land/water management -> 2.1. Site/area management -> habitat maintenance/protection
2. Land/water management -> 2.2. Invasive/problematic species control -> *Anolis sagrei*
2. Land/water management -> 2.3. Habitat & natural process restoration -> forest corridors
3. Species management -> 3.1. Species management -> Invasive & domestic species
3. Species management -> 3.2. Species recovery -> restore habitat and anole populations
4. Education & awareness -> 4.1. Formal education -> Local schools and community
4. Education & awareness -> 4.3. Awareness & communications -> tourists and public

Research Needed
(http://www.iucnredlist.org/technical-documents/classification-schemes)

Research Needed
1. Research -> 1.1. Taxonomy
1. Research -> 1.2. Population size, distribution & trends
1. Research -> 1.3. Life history & ecology
1. Research -> 1.6. Conservation Actions -> Mitigating deforestation and invasive species
2. Conservation Planning -> 2.1. Species Action/Habitat Recovery Plan
2. Conservation Planning -> 2.2. Area-based Management Plan
3. Monitoring -> 3.1. Population trends
3. Monitoring -> 3.4. Habitat trends

Additional Data Fields:

Distribution
Continuing decline in area of occupancy (AOO): Yes
Extreme fluctuations in area of occupancy (AOO): Yes
Estimated extent of occurrence (EOO) (km^2): 41
Continuing decline in extent of occurrence (EOO): Yes
Extreme fluctuations in extent of occurrence (EOO): No
Number of Locations: 1
Continuing decline in number of locations: No
Extreme fluctuations in the number of locations: No
Lower elevation limit (m): 0
Upper elevation limit (m): 74
Population
Number of mature individuals: 40,000-100,000
Continuing decline of mature individuals: Yes
Extreme fluctuations: Yes
Population severely fragmented: Yes
No. of subpopulations: 0
Continuing decline in subpopulations: No
Extreme fluctuations in subpopulations: No
All individuals in one subpopulation: Yes
Habitats and Ecology
Continuing decline in area, extent and/or quality of habitat: Yes

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